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ANNUAL SURVIVAL RATES OF FEMALE HOODED MERGANSERS AND WOOD DUCKS IN SOUTHEASTERN MISSOURI

KATIE M. DUGGER,[1,2,3] BRUCE D. DUGGER,[1,2] AND LEIGH H. FREDRICKSON[1]

ABSTRACT.—Successful conservation and management, particularly of harvested species, relies on accurate estimates of population demographics. In addition, estimates of survival and longevity allow more accurate modeling of evolutionary life-history trade-offs within and between species. We estimated survival rates for box nesting female Hooded Mergansers (*Lophodytes cucullatus*) and Wood Ducks (*Aix sponsa*) in southeastern Missouri during 1987–1997 and 1987–1993, respectively. Hooded Merganser survival rates varied annually and ranged from 0.42–1.0 ($\bar{x} = 0.66 \pm 0.04$). Wood Duck survival did not vary significantly over time and averaged 0.63 ($\pm$ 0.02). Mean annual survival rates and capture probabilities were similar for the two species ($\chi^2 = 0.49$, df = 1, $P > 0.05$; $\chi^2 = 0.02$, df = 1, $P > 0.05$). Annual variation in Hooded Merganser survival rates was an important component of this species' population ecology, but was not related to winter weather conditions, harvest rates, breeding season rainfall, or nesting parameters. Our female Wood Duck survival rates were higher than survival estimates for other adult females in the north-central subpopulation, but were comparable to some estimates for adult females that breed in southern and mid-Atlantic states. *Received 12 May 1998, accepted 5 Sept. 1998.*

Estimates of annual survival are important for comparative studies of life-history strategies between species (Krementz et al. 1989) and for modeling population demographics for conservation and management. Annual survival rate estimates are available for certain geese (tribe Anserini) and dabbling ducks (tribe Anatini) traditionally important to hunters (Johnson et al. 1992). Except for the Common Eider (*Somateria mollissima*; Krementz et al. 1996), survival estimates based on modern survival estimation procedures are completely lacking for most seaducks (tribe Mergini), despite increased harvest pressure in recent years (U.S. Fish and Wild. Serv., unpubl. data).

Hooded Mergansers (*Lophodytes cucullatus*) are among the least studied of all Mergini (Dugger et al. 1994). Attempts to estimate survival rates are difficult because of their low harvest rate, secretive behavior, year-round occurrence in low densities, and preference for forested wetlands. However, Hooded Mergansers nest in man-made boxes, and capture of these females can provide mark-recapture samples large enough to estimate survival rates (Dugger et al. 1994).

Over much of their range Hooded Mergansers occur sympatrically with Wood Ducks (*Aix sponsa*, tribe Anatini; Livezey 1986) providing an opportunity for comparison of survival estimates. The two species are similar in body size (HM, 540–725 g; WD, 530–680 g; Bellrose and Holm 1994), both nest in tree cavities, and both rely on forested wetlands

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during the breeding season. However, these species differ considerably in many aspects of their biology and might be expected to exhibit differences in annual survival rates. Hooded Mergansers are carnivorous, forage by diving, and exhibit delayed maturation (first breed at ≥2 years old; Dugger et al. 1994). In contrast, Wood Ducks are omnivorous, forage near the water's surface, and most breed as yearlings (Bellrose and Holm 1994). Based on the difference in age at first breeding and phylogeny (Krementz et al. 1997), we predict that Hooded Mergansers experience higher annual survival rates than Wood Ducks (Ricklefs 1973, Wittenberger 1979). In this paper we estimate annual survival rates of box nesting female Hooded Mergansers and Wood Ducks in southeastern Missouri and compare mean annual survival rates of these two species.

TABLE 1. The number of Hooded Merganser nesting attempts and nest success in southeastern Missouri 1987–1997.

Year	Nest attempts[a]	Nest success rate[b] (%)
1987	17	88.2
1988	32	84.4
1989	37	62.2
1990	35	77.1
1991	37	73.0
1992	59	35.6
1993	48	39.6
1994	64	51.5
1995	38	73.7
1996	43	58.1
1997	50	56.0

[a] Total number of nests initiated by Hooded Mergansers in southeast Missouri.

[b] Hooded Merganser nest success (number of successful nests/total number of nest attempts).

STUDY AREA AND METHODS

The study was conducted on the Duck Creek Wildlife Conservation Area (WCA) and Mingo National Wildlife Refuge (NWR) in southeastern Missouri. These adjoining areas comprise Mingo Swamp, the largest contiguous block of bottomland hardwood forest in Missouri (11,174 ha). For a detailed description of the habitat types available in Mingo Swamp see Heitmeyer and coworkers (1989). Approximately 85 boxes were available to nesting females in all years of the study on Mingo NWR, and 100–120 nest boxes were available for nesting birds on Duck Creek WCA during 1987–1993, and most nest boxes were equipped with predator guards to reduce predation by raccoons (*Procyon lotor*). After the nesting season in 1993, approximately 50 boxes were removed on Duck Creek WCA and the Wood Duck nesting study was terminated. Capture of Hooded Mergansers continued on both Mingo NWR and Duck Creek WCA through 1997.

Nest boxes were cleaned, repaired when necessary, and filled with wood chips before each nesting season. Hooded Mergansers and Wood Ducks were captured in nest boxes between 1 February and 15 August each year during 1987–1997 and 1987–93, respectively. We checked boxes at 2–4 week intervals and captured nesting females of both species during the third week of incubation. Unmarked females were banded with U.S. Fish and Wildlife Service leg bands, and band numbers of previously marked birds were recorded. All breeding females of both species captured in nest boxes were used in our analysis, including Wood Ducks that bred as yearlings. Although both Hooded Merganser and Wood Duck ducklings were web-tagged in boxes at hatching, sample sizes of known-age birds were too small to analyze by age class.

We constructed mark-recapture matrices for Hooded Mergansers (11 years) and Wood Ducks (7 years) and used Jolly-Seber mark-recapture models for open populations to estimate survival for both species (Pollock et al. 1990). Program JOLLY computes point estimates, their associated variances, goodness-of-fit tests, and likelihood ratio tests for five open population models (Pollock et al. 1990). We used model goodness-of-fit tests and likelihood ratio tests between models to select the model that provided the best fit for each data set (Pollock et al. 1990). We then compared Wood Duck and Hooded Merganser mean annual survival rates and capture probabilities using the program Contrast (Hines and Sauer 1989) and the methods described by Sauer and Williams (1989). All analyses were performed on an IBM computer under DOS.

Our analysis suggested time dependent variation was an important component of Hooded Merganser survival, so we attempted to identify factors that might be correlated with merganser annual survival rates. We correlated Hooded Merganser survival estimates for each year with annual harvest (USFWS, unpubl. data), winter weather conditions (rainfall, temperature) in the Mississippi Alluvial Valley, and rainfall in Mingo Swamp from March through September. We also correlated Hooded Merganser survival with the number of nesting attempts and nest success on Mingo NWR and Duck Creek WCA (Table 1). These reproductive variables might be expected to index local Hooded Merganser nesting density, and therefore represent the potential for permanent emigration from our study sites.

Although specific wintering areas for birds in our population are largely unknown, the Mississippi Alluvial Valley is the closest region with suitable wintering habitat, and females nesting in Mingo Swamp have been recovered from this region (Dugger et al. 1994). We used mean daily temperature and monthly rainfall totals recorded at two sites in each of three states (Arkansas, Mississippi, and Louisiana) October

TABLE 2. Annual survival estimates and associated capture probabilities for female Hooded Mergansers and Wood Ducks nesting in southeastern Missouri.

	Survival probability (SE)		Capture probability (SE)	
Year	Hooded Merganser	Wood Duck	Hooded Merganser	Wood Duck
1987	0.58 (0.17)	[a]		
1988	0.86 (0.16)	[a]	0.78 (0.19)	0.71 (0.07)
1989	1.00 (0.25)	[a]	0.43 (0.13)	0.77 (0.05)
1990	0.42 (0.11)	[a]	0.37 (0.12)	0.55 (0.05)
1991	0.97 (0.15)	[a]	0.53 (0.12)	0.48 (0.05)
1992	0.54 (0.12)	[a]	0.69 (0.13)	0.51 (0.06)
1993	0.55 (0.12)	[a]	0.59 (0.13)	0.66 (0.08)
1994	0.52 (0.13)		0.71 (0.14)	
1995	0.45 (0.12)		0.65 (0.15)	
1996			0.66 (0.16)	
Mean	0.66 (0.04)	0.63 (0.02)	0.60 (0.05)	0.61 (0.04)

[a] Recapture data from these years were available to estimate constant survival rate for Wood Ducks.

through January for each year (National Climatic Data Center) to index winter habitat conditions. We used total rainfall during March through September collected at Advance, Missouri (National Climatic Data Center) to index local habitat conditions during the breeding and post-breeding season when Hooded Mergansers are present in Mingo Swamp.

RESULTS

We used individual capture histories of 151 Hooded Merganser and 512 Wood Duck females to estimate annual survival. Model A, from Program JOLLY, with time-dependent capture probabilities and survival rates provided the best fit for the Hooded Merganser data ($\chi^2 = 19.61$, df = 12, $P > 0.05$). Model A also fit the Wood Duck data ($\chi^2 = 17.52$, df = 12, $P > 0.05$) as did Model B, a reduced parameter model with constant survival rates and time-dependant capture probability ($\chi^2 = 18.41$, df = 16, $P > 0.05$). The likelihood ratio test between Models A and B ($\chi^2 = 0.90$, df = 4, $P > 0.05$) suggested Model B provided the most parsimonious fit for the Wood Duck data. Jolly-Seber models estimate survival through sample k-2, and capture probability for samples 2 through k-1 (model A) or k (model B). Thus, we had 9 estimates of annual survival and capture probability for Hooded Mergansers (1987–1995) and 6 estimates of capture probability (1988–1992) for Wood Ducks with a single estimate of constant survival (Table 2). Hooded Merganser survival rates ranged from a low of 0.42 in 1990 to a high of 1.0 in 1989 with a mean of 0.66 (± 0.04 SE) with 95% confidence limits of 0.59–0.73 (Table 2). Wood Duck annual survival was 0.63 (± 0.02) with 95% confidence limits of 0.59–0.68 (Table 2). The mean annual survival of Hooded Mergansers was not significantly different than Wood Duck annual survival ($\chi^2 = 0.49$, df = 1, $P > 0.05$).

Capture probability for Hooded Mergansers varied annually from a low of 0.37 in 1990 to a high of 0.78 in 1988 (Table 2). Wood Duck capture rates also exhibited annual variation, ranging from 0.51 in 1992 to 0.77 in 1989 (Table 2). Mean capture probabilities did not differ between species ($\chi^2 = 0.02$, df = 1, $P > 0.05$). In addition, we observed no significant correlation between Hooded Merganser survival rates and annual harvest, winter weather conditions (temperature and rainfall), breeding season rainfall, or Hooded Merganser nesting parameters (all $P > 0.05$).

DISCUSSION

Hooded Merganser and Wood Duck annual survival estimates from our study were generally higher than those reported for other duck species (Johnson et al. 1992). However, because our estimates were for birds using nest boxes with some protection from predatory raccoons, comparisons with other species must be made with caution. Nevertheless, Hooded Mergansers in our study had substantially lower mean annual survival rates than the Common Eider ($\bar{x} = 0.87$; Krementz et al. 1996), the only other member of Mergini for which estimates are available. Yearly survival rates for Hooded Mergansers during 1988,

1989, and 1991 were comparable with those for Common Eiders (Krementz et al. 1996); rates for other years were substantially lower. Wood Duck survival in our study was higher than or comparable to other estimates available for female Wood Ducks (Johnson et al. 1986, Nichols and Johnson 1990, Kelley 1997), including estimates from a South Carolina box-nesting population ($\bar{x}$ = 0.55, Hepp et al. 1987). Wood Duck females are strongly philopatric to nest sites (nearly 100%), so mark-recapture survival estimates that include a measure of capture site fidelity (nest boxes in this case) can be comparable to band recovery estimates (Hepp et al. 1987). Whether our high survival rates reflect general regional differences in survival of eastern Wood Ducks (Nichols and Johnson 1990) or a survival benefit associated with box-nesting remains unclear. Wood Ducks breeding in Missouri are included in the "north-central" sub-population of Bowers and Martin (1975) and Kelley (1997), but exhibit survival rates much higher than band recovery estimates for adult females in this region (Kelley 1997). Our Wood Duck females exhibited survival rates most similar to adult females in the southern population of the Mississippi Flyway ($\bar{x}$ = 0.61; Kelley 1997) and the mid-Atlantic population of the Atlantic Flyway ($\bar{x}$ = 0.63; Kelley 1997).

Mean survival did not differ between Hooded Mergansers and Wood Ducks, although in three of nine years Hooded Merganser survival was higher than the constant rate estimated for Wood Ducks (Table 2). This is inconsistent with life-history theory which predicts that birds with delayed maturation should experience higher annual survival (Wittenberger 1979), but consistent with analyses showing survival rates are correlated with body size and breeding latitude in waterfowl (Arnold 1988). Maybe more important than the comparison of mean survival rates was our observation that annual variation was an important component of Hooded Merganser, but not Wood Duck, survival. Differences in diet, foraging method, and habitat requirements may make Hooded Mergansers more sensitive to local fluctuations in food resources or water conditions during reproduction or winter, with increased mortality or emigration during years when habitat conditions are poor. None of the harvest, breeding season rainfall, density-dependent factors, or winter weather variables we investigated were significantly related to variation in Hooded Merganser survival. However, we did not quantify food availability on the breeding grounds directly and because information on migration patterns and winter site fidelity for Hooded Mergansers is lacking we may not have compared our Hooded Merganser survival rates with the most appropriate winter or breeding season weather conditions. Very little information exists concerning Hooded Merganser foraging ecology or foraging habitat characteristics (Dugger et al. 1994), consequently, determining the climatic factors that index habitat conditions throughout the Hooded Merganser annual cycle will be difficult.

We believe our survival estimates for both species are unbiased, but some behavioral responses such as permanent emigration from the study area cannot be distinguished from "deaths" by Jolly-Seber models and can result in negatively biased survival estimates (Pollock et al. 1990). Wood Ducks are strongly philopatric (Hepp et al. 1987), but data are lacking to estimate philopatry for Hooded Mergansers or to make direct quantitative comparisons with Wood Ducks. We believe that Hooded Mergansers are strongly philopatric to general nesting areas (e.g., Zicus 1990), but not as philopatric as Wood Ducks to specific nesting boxes. Factors that might have caused Hooded Merganser females to have left the study site or chosen not to nest in boxes in subsequent years (low nest success or high breeding density) were not correlated with annual survival as we might expect if permanent emigration were common. Furthermore, in Minnesota, distances moved by Hooded Mergansers between nesting sites each year were not related to nest success (Zicus 1990), suggesting that variation in nest success does not affect philopatry. Habitat conditions in Mingo Swamp could have affected Hooded Merganser use of boxes, but it is unlikely that these effects would be permanent. Finally, we do not believe that nest boxes were limiting for Hooded Mergansers or that competition for nest sites led to higher permanent emigration by Hooded Mergansers from Mingo Swamp. Hooded Merganser populations were substantially lower than Wood Duck populations each year (Dugger 1991)

and the annual number of Hooded Merganser nest attempts remained low in relation to box availability. In addition, Hooded Mergansers initiate nests on average 3–4 weeks earlier than Wood Ducks, thereby reducing the potential for nest site competition between the two species (Dugger et al. 1994).

Overall mean Hooded Merganser survival in this study was lower than a previous estimate (Dugger et al. 1994), and this earlier analysis did not detect any significant annual variation in survival rates. As more data were collected and added to the analysis, estimate precision increased, mean annual survival decreased, and annual variation became an important component of Hooded Merganser survival. The increased variation in annual survival estimates and changes in the long-term mean associated with additional years of study on Hooded Mergansers illustrate the importance of long-term data sets. Continued banding effort and more information concerning Hooded Merganser habitat use, foraging ecology, and age-specific survival rates are needed to understand the factors affecting annual variation in survival of this species.

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COMPARATIVE NEST SITE HABITATS IN SHARP-SHINNED AND COOPER'S HAWKS IN WISCONSIN

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ABSTRACT.—From an analysis of nest site habitat data at 24 Sharp-shinned Hawk (*Accipiter striatus*) and 52 Cooper's Hawk (*A. cooperii*) nests in Wisconsin, we conclude that Cooper's Hawks tend to nest in stands with lower densities of taller and larger trees than do Sharp-shinned Hawks, and that Cooper's Hawks also tend to nest in sites with a greater proportion of hardwood cover than Sharp-shinned Hawks. Significant interspecific differences were found in combined habitat types (hardwoods, mixed conifer-hardwoods, and conifer plantations) for nest tree height and nest tree DBH (diameter at breast height); nest height; nest height relative to tree height; canopy height; canopy cover; tall shrub density; tree density; and mean DBH. Nest sites of the two species were similar in terms of understory canopy cover, ground cover, low shrub index, understory tree density, basal area, distance to nearest forest opening, and distance to water. We detected few significant intraspecific differences in nest site habitat, and these only in the Cooper's Hawk. *Received 23 Oct. 1997, accepted 4 Nov. 1998.*

Although the Sharp-shinned Hawk (*Accipiter striatus*) and the Cooper's Hawk (*A. cooperii*) breed sympatrically in many parts of the United States and southern Canada, their nest site habitats have been compared in only four published quantitative studies. These congeners are sometimes assumed to partition nesting habitat by way of interspecific competition and/or predation (Siders and Kennedy 1996). With one exception in Missouri (Wiggers and Kritz 1991), these studies were conducted in the western United States (Oregon: Reynolds et al. 1982, Moore and Henny 1983; New Mexico: Siders and Kennedy 1996).

Such geographically restricted results may be difficult to extrapolate to other areas of sympatry because of regional differences in vegetational composition and structure. Each of the previously published comparisons of these hawks' nest site habitats was derived from upland forests with relatively homogeneous vegetation, principally montane conifer forests in New Mexico and Oregon, and conifer plantations or oak-hickory forests in Missouri. Our study area (Fig. 1) was the state of Wisconsin (145,000 km^2). The ecologically diverse set of available woodland nesting habitats on this statewide scale includes boreal conifer forests (plus conifer swamps of boreal affinity over much of the state), conifer plantations, mixed conifer-hardwood forests, purely deciduous woodlands on upland and lowland sites, and highly fragmented or urban woodlands (Rosenfield et al. 1996) as well as extensive forests. For further details on Wisconsin forests see Curtis (1959).

Potentially conflicting results among past studies may also limit their utility in unstudied areas of sympatry. In New Mexico, for example, Siders and Kennedy (1996) found significant differences between Sharp-shinned Hawks and Cooper's Hawks in the majority of nest site variables tested, while in Oregon, both Reynolds and coworkers (1982) and Moore and Henny (1983) found few discernible differences in nest site characterisitics between these accipiters. Furthermore, Siders and Kennedy (1996) have suggested that interpretations of previous results may be hampered by small sample sizes, especially for Sharp-shinned Hawks ($n < 18$ nests in prior studies), and by possible biases in nest search methods or methods of selecting search areas.

We compare habitat at 24 Sharp-shinned Hawk nests and 52 Cooper's Hawk nests in Wisconsin, 1980–1994, all discovered by unbiased means. Previous comparative work on nest site habitats of these two hawks has emphasized interspecific differences within relatively uniform habitat types. We expand this

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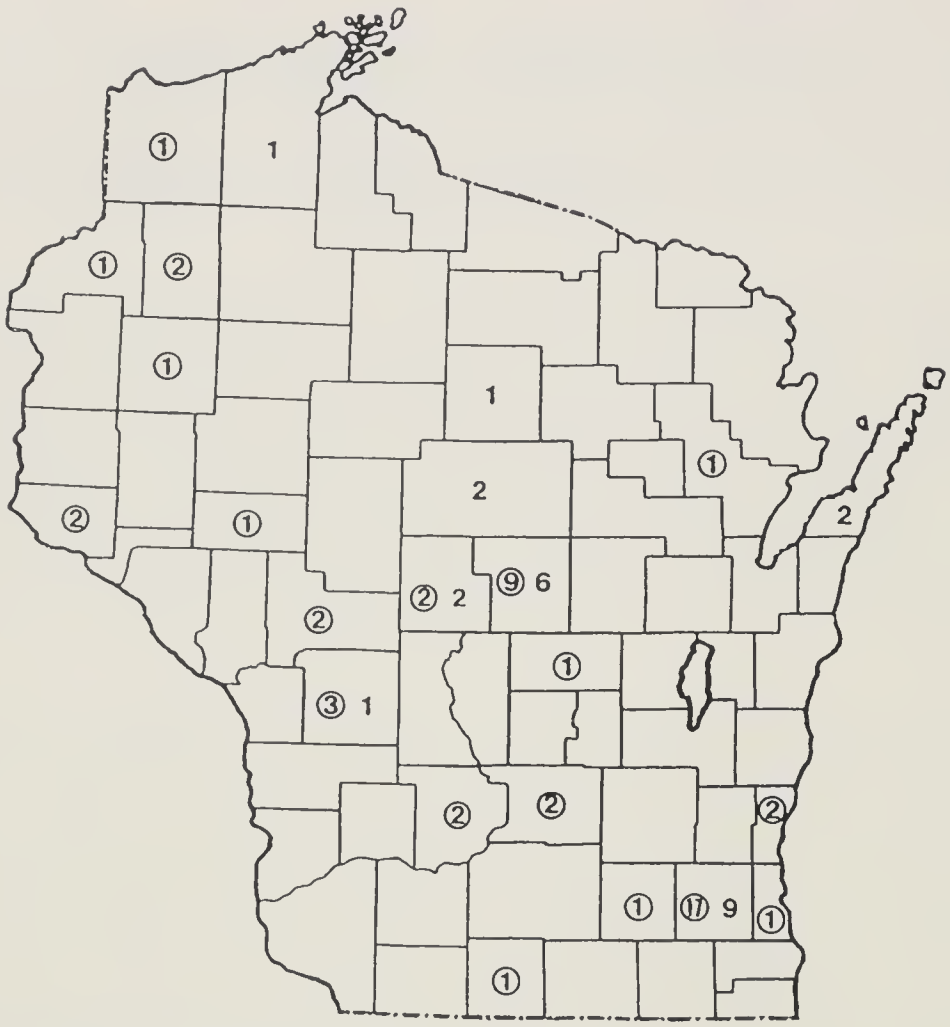

FIG. 1. Distribution by county of nest sites sampled for *Accipiter cooperii* (circled) and *A. striatus* (not circled) in Wisconsin.

emphasis to include intraspecific similarities as well as interspecific differences across habitat types (i.e., combined habitats) at a landscape scale. Intraspecific nest site features held in common across habitat types may aid land management agencies in assessing and conserving a range of usable breeding habitats for Sharp-shinned and Cooper's hawks. Our results seem timely and pertinent to the recent Birds in Forested Landscape project for North America (Cornell Lab of Ornithology), which focuses in part on the nesting habitats of these two hawks, and is designed to develop management and conservation strategies on their behalf (Anonymous 1997).

METHODS

Nest locations.—Nest site locations were considered unbiased if they were discovered by one of two methods: (1) incidental or random locations obtained by cooperators during any activity other than searching for accipiter nests, and (2) locations resulting from Cooper's Hawk density studies in which objectively drawn study areas were completely searched regardless of their perceived suitability for nesting and without foreknowledge of current or historical nest sites on these areas. By these methods, we located Cooper's Hawk nests in Wisconsin (see Fig. 1) on 52 widely separated, independent nesting areas, as defined in Rosenfield and Bielefeldt (1992, 1996). All 24 Sharp-shinned Hawk nests occurred in independent nesting areas; therefore each was included in our analyses.

Data collection and analyses.—Habitat measurements (Table 1) were made postfledging at each nest site within a 0.04 ha circular plot centered on the nest tree following the technique of James and Shugart (1970) as modified by Titus and Mosher (1981).

All variables were tested for normality with Lilliefors test; further statistical analyses were performed on SYSTAT (Wilkinson 1992). *t*-tests were used exclusively to examine interspecific differences among seven habitat varables that exhibited normal distributions in combined habitats (i.e., tree height, tree DBH, nest height, nest percent, canopy height, total canopy, and mean DBH; Table 2). We used the Mann-Whitney *U*-test for all other inferential comparisons because all other variables were not normally distributed.

To examine inter- and intraspecific differences and

TABLE 1. Habitat variables and measurement techniques at *Accipiter striatus* and *A. cooperii* nest sites in Wisconsin.

Variable	Description
Tree height	Height (m) of nest tree (Haga altimeter)
Tree DBH	Diameter (cm) at breast height of nest tree
Nest height	Height (m) of nest (meter tape or Haga altimeter)
Nest percent	(Nest height/Tree height) × 100
Canopy height	Mean height (m) of five canopy trees in study plot (Haga altimeter)
Total canopy	Percent of area over study plot occluded by overstory foliage[a]
Deciduous can.	Percent of area over plot (*not* of total canopy) occluded by deciduous overstory foliage[a]
Coniferous can.	Percent of area over plot occluded by evergreen overstory foliage[a]
Understory can.	Percent of area over plot occluded by understory foliage[a]
Ground cover	Percent of ground in plot covered by ground-layer foliage[a]
Shrub density	Index of tall shrubs < 3 cm DBH and ≥ shoulder height[b]
Shrub index	Index of low shrubs < 3 cm DBH between knee and shoulder height[b]
Tree density	Number of canopy trees ≥ 9 cm DBH per hectare
Under. dens.	Number of understory trees ≥ 9 cm DBH per hectare
Basal area	m^2/ ha of canopy trees
Mean DBH	Mean DBH (cm) of canopy trees in study plot
Dist. to water	Distance (m) to nearest permanent water source (pacing or USGS 7.5 min. quadrangles)
Dist. to open.	Distance (m) to nearest forest opening ≥ 5 ha (pacing or USGS 7.5 min. quadrangles)

[a] 40 ocular tube readings.
[b] Sum of four plot radii.

similarities among habitat types, we separated our nest site samples into three categories based on trees present within the 0.04 ha plot. We first divided nest site samples between those occurring within conifer plantations and those not in plantation habitats. (While deciduous trees occurred in some conifer plantations, no nest sites occurred in hardwood plantations.) We then divided non-plantation nest sites into those situated in pure hardwood stands (where no trees within the study plot were conifers) and those in mixed conifer-hardwood stands. In keeping with our statewide sample, these three habitat categories should be construed as physiognomic types that do not necessarily exhibit other internal similarities in vegetational attributes. In hardwood stands, for example, dominant or prominent tree species might include oaks (*Quercus* spp.), maples (*Acer* spp.), aspen (*Populus* spp.), and other species of varied ages, management histories, and moisture regimes. Mixed woodlands might include lowland conifers such as tamarack (*Larix larcina*) and black spruce (*Picea mariana*) or upland conifers such as pines (*Pinus* spp.) as well as deciduous species. For compositional variety among nest tree species (and scientific names) see Table 3.

Because there was only one pure hardwood site used by Sharp-shinned Hawks, we examined interspecific differences only within conifer plantations and mixed conifer-hardwood habitats. Likewise, we could only test for intraspecific differences between mixed and plantation habitats among Sharp-shinned Hawk nest sites. We used the nonparametric Kruskall-Wallis test to examine interspecific differences among the three habitat types used by Cooper's Hawks. Because of the number of multiple univariate comparisons (Table 2), we calculated that an alpha of 0.001 was the appropriate level of significance for both inter- and intraspecific inferences (Sokal and Rohlf 1981).

RESULTS

The majority of the 18 nest site variables compared for Sharp-shinned and Cooper's hawks in combined habitats showed statistically significant interspecific differences (Table 2). Nest tree DBH in conifer plantations, and nest height and canopy height in mixed conifer-hardwood stands were significantly different between species across uncombined habitat types (Table 2).

Of the 18 variables examined only four exhibited significant intraspecific differences across habitat types, and only in Cooper's Hawk (Table 2). Although intraspecific nest site selection itself might vary among habitats, we speculate that these statistical differences instead are attributable to inherent vegetational contrasts among habitat types as circumscribed here. In the most transparent example, cross-habitat intraspecific differences in percentages of coniferous and deciduous canopy covers at Cooper's Hawk nest sites in hardwood stands versus pine plantations (Table 2) are a predictable outcome of our habitat categories. The more interesting result of intra-

TABLE 2. Mean values of habitat variables measured at *Accipiter striatus* and *A. cooperii* nest sites in Wisconsin.

Variable	*A. striatus* (mean ± SE)		
	Combined	Mixed	Plantation
	(n = 24)[a]	(n = 11)	(n = 12)
Tree height (m)	15.1 ± 0.6	14.8 ± 0.6	15.8 ± 1.0
Tree DBH (cm)	23.8 ± 1.4	26.2 ± 2.3	21.4 ± 1.6
Nest height (m)	9.1 ± 0.6[b]	7.9 ± 0.7[b]	10.4 ± 0.8
Nest percent (%)	59.7 ± 2.7[b]	54.1 ± 4.3[b]	65.5 ± 2.7
Canopy height (m)	15.2 ± 0.6	15.0 ± 0.6	15.8 ± 0.9
Total canopy (%)	76.5 ± 2.3	74.3 ± 2.5	80.4 ± 3.3
Deciduous can. (%)	15.2 ± 4.4	24.3 ± 7.7	3.8 ± 1.7
Coniferous can. (%)	61.3 ± 5.6	50.0 ± 8.1	76.7 ± 3.6
Understory can. (%)	32.7 ± 5.8	42.7 ± 8.7	19.8 ± 6.2
Ground cover (%)	39.0 ± 6.2	53.4 ± 8.0	22.9 ± 7.8
Shrub density	61.6 ± 9.3	73.4 ± 17.5	50.3 ± 9.2
Shrub index	90.3 ± 13.7	79.0 ± 18.4	98.1 ± 21.9
Tree density (trees/ha)	1071 ± 95[c]	914 ± 96	1037 ± 131[c]
Under. dens. (trees/ha)	334 ± 71[b]	375 ± 120[b]	231 ± 57
Basal area (m^2/ha)	28.9 ± 3.0[c]	22.7 ± 2.7	37.5 ± 3.9[c]
Mean DBH (cm)	17.6 ± 0.9[c]	16.9 ± 1.2	19.1 ± 1.3[c]
Dist. to water (m)	260 ± 71	88 ± 28	440 ± 120
Dist. to open. (m)	58.9 ± 16.2	72.7 ± 26.2	50.8 ± 21.8

* $P \leq 0.001$.
** $P \leq 0.0005$.
[a] Combined data for *A. striatus* includes one hardwood nest site in addition to mixed and plantation nest sites.
[b] Missing data at one nest site (n = 23 combined, n = 10 mixed).
[c] Missing data at one nest site (n = 23 combined, n = 11 plantation).

specific analyses may lie in the variables that did not differ significantly across habitats, such as nest tree height, nest height, canopy height, and mean tree DBH—each of which differed between species (see Discussion).

For combined habitats, Cooper's Hawks nested in a wider array of tree species than Sharp-shinned Hawks (Table 3). This variation however, occurred mostly within hardwood sites; within mixed stands and conifer plantations Sharp-shinned Hawks used a greater variety of tree species. Of the coniferous nest trees used by Cooper's Hawks (n = 29), only *Pinus* was represented in this sample, while Sharp-shinnned Hawks (n = 23) used five genera. With only one exception [a Cooper's Hawk nest in a white ash (*Fraxinus americana*)], both species consistently used conifers for nesting in mixed sites where both hardwoods and conifers were present in the canopy. For both species, nest trees in conifer plantations were all conifers, despite the presence of canopy-level hardwoods in 60% of Cooper's Hawk and 42% of Sharp-shinned Hawk plantation sites.

DISCUSSION

Our comparative analyses of nest site habitat at 52 Cooper's Hawk and 24 Sharp-shinned Hawk nests in Wisconsin did not provide data on nest site use relative to availability, and we cannot contend that numbers of nests in our three habitat categories are necessarily proportional to use of these habitat types. Nevertheless, our sample involves independent nests discovered by unbiased means on a statewide scale in compositionally diverse woodland habitats: upland and lowland sites; coniferous, hardwood, and mixed forests; urban and rural woodlands of varied sizes; and both managed and unmanaged forests including conifer plantations. Thus we suggest that our data set provides a reasonably thorough and representative sample of the range of nest site habitats used by these hawks in Wisconsin.

If interspecific differences in nest site characteristics of these congeners occur on a finer within-habitat scale, as some prior work has indicated (Siders and Kennedy 1996), then

TABLE 2. Extended.

A. cooperii (mean ± SE)				Interspecific differences			Intraspecific differences	
Combined	Hardwood	Mixed	Plantation	Combined	Mixed	Plantation	*A. striatus*	*A. cooperii*
(n = 52)	(n = 22)	(n = 10)	(n = 20)					
19.1 ± 0.6	20.5 ± 1.0	17.5 ± 0.8	18.1 ± 0.8	**				
32.6 ± 1.2	36.2 ± 1.6	29.7 ± 3.1	30.0 ± 1.6	**		*		
13.1 ± 0.4	13.3 ± 0.7	13.2 ± 0.7	12.9 ± 0.5	**	*			
69.8 ± 1.4	66.1 ± 2.9	75.0 ± 1.9	72.3 ± 2.1	*				
19.5 ± 0.5	20.9 ± 0.9	18.6 ± 0.6	18.3 ± 0.7	**	*			
84.9 ± 1.3	86.3 ± 2.1	79.3 ± 3.4	86.3 ± 1.8	*				
54.9 ± 4.8	86.1 ± 2.1	46.3 ± 7.3	24.8 ± 5.9	**				**
30.0 ± 4.5	0.1 ± 0.1	33.0 ± 6.2	61.5 ± 5.5	**				**
37.8 ± 3.6	48.8 ± 5.1	30.3 ± 6.0	29.5 ± 6.1					
47.8 ± 3.0	53.6 ± 4.2	54.5 ± 5.7	38.1 ± 5.2					
30.0 ± 4.4	26.2 ± 5.4	38.6 ± 15.8	29.9 ± 6.4	*				
71.5 ± 8.4	65.5 ± 10.7	60.0 ± 15.2	84.0 ± 16.8					
623 ± 48	438 ± 38	623 ± 103	826 ± 87	**				*
307 ± 28	340 ± 40	383 ± 68	233 ± 44					
31.6 ± 2.8	27.4 ± 3.4	24.0 ± 2.0	39.9 ± 5.8					*
25.6 ± 0.9	27.4 ± 1.5	22.4 ± 1.7	25.2 ± 1.4	**				
320 ± 56	412 ± 87	277 ± 111	468 ± 115					
56.7 ± 8.6	86.8 ±17.4	33.9 ± 9.6	39.1 ± 7.3					

differences might also exist on a coarser scale among more broadly defined and heterogeneous habitat types. Such differences might furthermore emerge on a landscape scale among woodland habitats in general.

The variables we measured are not independent indicators of interspecific differences in nest site habitat; many of them seem to be related to stand age or successional stage. Tree age was not measured in this study, but it appears that Cooper's Hawks tended to use older stands with a lower density of taller and larger trees. Sharp-shinned Hawks, on the other hand, tended to use younger stands with a higher density of smaller, shorter trees. Reynolds and coworkers (1982) and Moore and Henny (1983) also have suggested that differences in accipiter nest site habitat are correlated with stand age or successional stage, with Cooper's Hawks using older stands than Sharp-shinned Hawks.

Interspecific differences in combined habitats seldom seem the result of contrasting proportions of habitats used on the intraspecific level. The lower percent coniferous canopy in combined Cooper's Hawk habitats versus Sharp-shinned Hawk habitats (30% vs 61%, $P < 0.0005$; Table 2) appears to be the result of the disproportionate number of Cooper's Hawk sites in hardwoods (42% of 52 nests) compared to the one Sharp-shinned Hawk at a hardwood site (4% of 24 nests). The difference in deciduous canopy cover between Cooper's Hawks versus Sharp-shinned Hawks in combined habitats (55% vs 15%, $P < 0.0005$; Table 2) also seems to be a result of contrasting proportions of habitat use.

In addition to having proportionally more nests in hardwood stands, Cooper's Hawks nested in conifer plantations that had substantially greater deciduous canopies than those used by Sharp-shinned Hawks (25% vs 4%; Table 2). In mixed conifer-hardwood habitats the deciduous canopy cover percentage again was greater for Cooper's Hawks than for Sharp-shinned Hawks (46% vs 24%; Table 2). Although neither of these within-habitat differences was statistically significant, they are clearly consistent with a significant difference in deciduous canopy in combined habitats. On a landscape-scale continuum from Wisconsin's northern coniferous forests (plus conifer plantations) to mixed and southern deciduous woodlands (see Curtis 1959), nest habitat thus appears to be comprised more of deciduous sites or elements for the Cooper's Hawk and coniferous elements for the Sharp-shinned Hawk, albeit with considerable overlap in

TABLE 3. Nest tree species used by *Accipiter striatus* and *A. cooperii* in Wisconsin.

Tree species	*A. striatus*				*A. cooperii*			
	Hardwood	Mixed	Plantation	Total	Hardwood	Mixed	Plantation	Total
Red Oak *Quercus rubra*					7			7 (13%)
Black/Hill's Oak *Q. velutina/ellipsoidalis*	1			1 (4%)	5			5 (10%)
White Oak *Q. alba*					1			1 (2%)
Red Maple *Acer rubrum*					2			2 (4%)
Sugar Maple *A. saccharum*					2			2 (4%)
Basswood *Tilia americana*					1			1 (2%)
Paper/White Birch *Betula papyrifera*					1			1 (2%)
American Elm *Ulmus americana*					1			1 (2%)
Big Tooth Aspen *Populus grandidentata*					1			1 (2%)
White Ash *Fraxinus americana*						1		1 (2%)
White Pine *Pinus strobus*		2		2 (8%)		6	16	22 (42%)
Jack Pine *Pinus banksiana*		1	3	4 (17%)		3	1	4 (8%)
Red Pine *Pinus resinosa*			3	3 (13%)			2	2 (4%)
Scotch Pine *Pinus sylvestris*			1	1 (4%)			1	1 (2%)
Norway Spruce *Picea abies*			4	4 (17%)				
Black Spruce *P. mariana*		1	1	2 (8%)				
Balsam Fir *Abies balsamea*		3		3 (13%)				
White Cedar *Thuja occidentalis*		2		2 (8%)				
Tamarack *Larix laricina*		2		2 (8%)				
Snag					1			1 (2%)
Total	1 (4%)	11 (46%)	12 (50%)	24	22 (42%)	10 (19%)	20 (38%)	52

mixed forests. This divergence seems unapparent in western montane environments (Reynolds 1983, Fischer 1986).

Siders and Kennedy (1996) also found that Cooper's Hawks used significantly taller nest trees with greater diameters and nest sites with lower tree densities than did Sharp-shinned Hawks. However, they reported that Sharp-shinned Hawk nest sites had significantly higher basal areas and canopy closures than did those of Cooper's Hawks. Reynolds and coworkers (1982) found, as we did that Cooper's Hawks had greater nest heights in eastern Oregon, and used habitats at lower tree densities in northwestern Oregon than did Sharp-shinned Hawks. As did Siders and Kennedy (1996), they found that Sharp-shinned Hawk nest sites had greater canopy closure than those of Cooper's Hawks. Moore and Henny (1983) noted that Cooper's Hawk nests were significantly higher than those of Sharp-shinned Hawks, but again in contrast to our results they found that Sharp-shinned Hawk nest sites had significantly higher canopy closure than sites used by Cooper's Hawks.

It seems that significantly higher tree densities at Sharp-shinned Hawk nest sites would usually lead to significantly greater canopy closure, as reported for mostly coniferous habitats in New Mexico and Oregon, but this was not the case for combined habitats in Wisconsin. Our results show lesser canopy closure in association with greater tree densities at nest sites of Sharp-shinned versus Cooper's hawks (Table 2). This seeming contradiction is probably the result of disproportional use of broad-leaved hardwood forests (vs needle-leaved conifer forests) by Cooper's Hawks and consequent effects of leaf surface on measures of canopy closure. Overstory canopy measures might also be influenced by lower foliage densities (e.g., tamarack) or strongly conical growth forms (e.g., black spruce) in some nest tree species used by Sharp-shinned Hawks (Table 3).

In Missouri, Wiggers and Kritz (1991) used the most similar set of habitat measures and techniques for analyzing those measures, yet they reported no significant differences in nest site characteristics for these two accipiters. However, they divided their nest sites into habitat types differently than we did and were able to make interspecific comparisons only for pine dominated habitat ("> 50% of overstory trees were pines"). Still, with small data sets (Table 2) and the same alpha level (0.001) we detected significant differences in nest height and average canopy height for nest sites in mixed conifer-hardwoods, and in nest tree DBH in conifer plantations. Wiggers and Kritz (1991) reported significant intraspecific differences between pine habitat and hardwood habitat for Cooper's Hawks; had they combined these habitats they might have found overall interspecific differences as we did. Their ability to detect significant differences may also have been hampered by the fact that 87% of their nests were located by searching habitat (especially coniferous habitat) that was assumed *a priori* to be suitable for one or both species (Siders and Kennedy 1996). Consequently, 92% of nests in conifers (n = 50) and 77% of all nests (n = 60) were situated in pine plantations of similar age and vegetational structure.

In Wisconsin there appear to be numerous interspecific differences in nest site habitats of Cooper's and Sharp-shinned hawks. Such interspecific differences, within and across divergent habitat types, may provide guidance in identifying and managing the respective nesting habitats of these birds, one or both of which have been listed as species of conservation concern in several midwestern states (Rosenfield et al. 1991, Rosenfield and Bielefeldt 1993). Many of the nest tree and nest site variables differing significantly between species (tree heights, densities, diameters, and coniferous components) are routinely and easily estimated measures of woodland habitats among resource managers.

Intraspecific analyses of nest site variables across habitat types may also be useful to management and conservation. Significant intraspecific differences among habitats in the Cooper's Hawk would seem to portray the breadth of acceptable nesting habitat(s). Variables that do not differ intraspecifically across habitat types (e.g., nest tree height or mean DBH of nest site trees) may serve as focal points for managers in identifying potentially usable nesting habitats, whether or not these features actually provide proximate cues to nest site use for the birds themselves.

We examined habitat characteristics only at the nest tree level and in a small area (0.04

ha) immediately surrounding the nest. We did not deal with other habitats used by these accipiters such as hunting areas or non-breeding habitats. Recent studies of nest site habitat in the Cooper's Hawk in North Dakota (M. Nenneman, pers. comm.) suggest that existing analyses of breeding habitats from disparate areas and woodland types may not be generalizable to other regions. Management implications drawn from our Wisconsin data should therefore be cautious.

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MADAGASCAR FISH-EAGLE PREY PREFERENCE AND FORAGING SUCCESS

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ABSTRACT.—We investigated Madagascar Fish-Eagle (*Haliaeetus vociferoides*) foraging ecology to determine prey preference and the effect of fish abundance on fish-eagle foraging rates and foraging success. We observed fish-eagle foraging behavior at nine lakes in western Madagascar from May to August 1996. We sampled the fish population at each lake using gill nets and recorded fish weights and species. Introduced tilapia, *Oreochromis* spp. and *Tilapia* spp., made up the majority of both the gill net (66.3%) and fish-eagle catch (64.7%) in similar proportion, suggesting that the fish-eagle is an opportunistic predator. Consequently, replacement of native fish species by exotics probably has not been detrimental to the island's fish-eagle population. Male fish-eagle foraging success was positively correlated ($P < 0.001$) with number of fish species, suggesting that fish species diversity may affect fish-eagle foraging effectiveness. *Received 24 July 1997, accepted 2 Nov. 1998.*

Prey availability influences breeding area selection (Swenson et al. 1986), breeding density (Dzus and Gerrard 1989), reproductive success (Grubb 1995), and date of breeding (Hansen 1987) in Bald Eagles (*Haliaeetus leucocephalus*) and productivity in White-tailed Eagles (*Haliaeetus albicilla*; Helander 1985). It also affects distribution and density of Bald Eagles at wintering sites (Griffin and Baskett 1985, Sabine and Klimstra 1985, Keister et al. 1987, Hunt et al. 1992b) and migratory stopovers (Fraser et al. 1985, Bennetts and McClelland 1991).

Although prey availability is clearly important to *Haliaeetus* eagles, there has been little research aimed at quantitatively determining prey abundance and its effects on prey selection, foraging rates, and foraging success in the genus. Steenhof (1976), Mersmann (1989), and Hunt and coworkers (1992a) used gill nets to inventory relative fish abundance and determined that the most frequently netted fish species made up the greatest proportion of the Bald Eagle's diet. Wintering Bald Eagles in New Mexico fed most frequently on big game carrion when it was the most abundant prey source (Grubb 1984). There is a positive relationship between prey abundance and foraging success of wintering Bald Eagles both between locations (Stalmaster and Plettner 1992) and between years (Brown 1993). Knight and Knight (1983) found a negative correlation between search time and relative prey abundance of Bald Eagles wintering in Washington, but Mersmann (1989) did not find a correlation between Bald Eagle foraging rates and gill net catch rates on the northern Chesapeake Bay.

Langrand and Meyburg (1989) and Razafindramanana (1995) have documented fish species eaten by Madagascar Fish-Eagles (*Haliaeetus vociferoides*), but there has been no previous attempt to quantitatively assess the eagle's diet. The objectives of this study were (1) to describe the diet and foraging behavior of the Madagascar Fish-Eagle at lakes in western Madagascar, (2) to determine fish-eagle prey preference, and (3) to determine whether fish-eagle foraging rates and foraging success are dependent on prey abundance.

STUDY AREA AND METHODS

We observed Madagascar Fish-Eagle foraging ecology from 22 May to 4 August 1996 at nine lakes in the Tsiribihina, Manambolo, and Beboka river drainages between the Bongolava escarpment and the Mozambique Channel in western Madagascar (Table 1). We selected lakes that we felt would offer the best conditions for viewing eagles throughout the day from among 32 lakes with resident Madagascar Fish-Eagle pairs that we studied in 1995 (Berkelman 1997).

We observed fish-eagle foraging behavior throughout daylight hours from 06:00 to 18:00 (GMT + 3 h) for six or seven days at each lake. We recorded both

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TABLE 1. Lakes included in Madagascar fish-eagle foraging ecology study in western Madagascar, May–August, 1996.

Lake	Coordinates	Dates observed
Ambereny	18° 55′ S, 44° 23′ E	22–28 May
Bejijo	19° 13′ S, 44° 32′ E	30 May–5 June
Ankazomena	19° 42′ S, 45° 23′ E	8–15 June
Asonjo	19° 50′ S, 45° 26′ E	16–23 June
Ampamandrika	19° 46′ S, 44° 34′ E	27 June–3 July
Befotaka	19° 1′ S, 44° 24′ E	7–12, 20 July
Masama	18° 50′ S, 44° 27′ E	13–19 July
Bevoay	19° 9′ S, 44° 24′ E	22–28 July
Tsiandrora	18° 58′ S, 44° 38′ E	30 July–4 August

observer-time, the number of hours spent observing eagles, and eagle-time, the product of observer-time and the number of eagles observed during each hour, for each lake. At the three lakes that had more than one resident fish-eagle pair, we randomly selected one of the pairs for observation during the period. We watched from an inflatable kayak or from the shore using 10 × 50 binoculars and a 15–45 × spotting scope on a rifle mount. We concentrated on the resident eagle pair while also noting the behavior of any other eagles that we could see, including immatures and other adults that were associated with the resident pair. We distinguished adult fish-eagle sexes by the smaller size and higher pitched vocalizations of the males. We distinguished adults from immatures by their vocalizations and by the completely white plumage on the tails and the faces of the adults (Langrand and Meyburg 1989).

We recorded prey searches when eagles flew low over the water looking down (Stalmaster and Plettner 1992) and kills when they picked up a fish from the water. We also noted instances of fish-eagles scavenging dead fish from the shoreline or pirating fish from Black Kites (*Milvus migrans*). We identified fish to species whenever possible. If we could not identify the fish while the eagle was in flight, we looked for prey remains on the ground beneath the eagle's feeding perch.

We set two monofilament gill nets for 3 h at each lake starting at 06:00–06:15. The gill nets had a foam core float rope and a lead core bottom rope, were 0.91 m deep by 45.7 m long, and were divided into three 15.2 m panels of 2.5, 3.8, and 5.1 cm mesh size. We attached floats to the first net and set it parallel to the shore in water about 0.9 m deep. We set the second net on the bottom, parallel to the shore, in water about 1.8 m deep. Thus, we sampled fish from among the first and second 0.9 m of the water column. If the lake was less than 1.8 m deep, we set the second net in the deepest water within 200 m of where we had set the first net. We placed nets adjacent to the nest or, where we did not find a nest ($n = 1$), adjacent to a frequently used perch. We believed that these sites were representative of fish-eagle foraging areas because we observed the eagles forage most frequently within 300 m of the nest at eight of the nine lakes.

We identified each fish caught in the gill nets using keys (Arnoult 1959, Kiener 1963, Glaw and Vences 1994) and weighed it to the nearest g and measured total fish length to the nearest cm. We combined the data for the three days that we sampled each lake (nine hours total) and calculated total number of fish caught, total weight (kg) of fish catch, average fish weight (g), and number of species. We did not include fish that weighed over 1.5 kg in these calculations because we did not see fish-eagles capture larger fish.

We conducted the χ^2 test of equal proportions to determine if fish-eagle use of fish species was different from expected use based on gill net samples using SAS on an IBM compatible computer (PROC FREQ, SAS Institute Inc. 1990). We excluded unidentified prey from this analysis. After finding a significant ($P < 0.05$) overall difference, we tested the hypothesis of no difference between use and availability of each fish species, following Marcum's and Loftsgaarden's (1980) technique. We calculated Spearman correlation coefficients between fish-eagle foraging variables and fish variables (PROC CORR, SAS Institute Inc. 1990). For all analyses, we used an overall confidence level of $\alpha = 0.05$ and a confidence level of α/k, where k was the number of significance values calculated, following the Bonferroni approach (Miller 1966).

RESULTS

Foraging behavior.—There were extra adult Madagascar Fish-Eagles associated with three pairs and immatures with another three of the nine resident pairs that we studied. Altogether, we observed 11 adult males, 10 adult females, and 3 immatures.

Hunting methods were similar to those used by other sea eagles (Brown 1980, Love 1983, Stalmaster 1987). The fish-eagles we observed hunted from perches and either stooped directly from a perch or searched low over the water, generally returning to perch within 5

TABLE 2. Male Madagascar Fish-Eagle foraging at nine lakes in western Madagascar, May–August, 1996.

Variable	$\bar{x}$ (n = 11)	SE
Searches	36.7	8.0
Kills	5.9	1.7
Searches/hour/eagle	0.68	0.15
Kills/hour/eagle	0.10	0.03
Kills/search	0.16	0.04

TABLE 3. Number of fish, total fish weight, average fish weight, and number of fish species caught in gill nets at nine lakes occupied by Madagascar Fish-Eagles in western Madagascar, May–August, 1996.

Variable	$\bar{x}$	SE	Range
Number of fish	30.1	7.3	4–66
Total weight, kg	4.6	1.6	0.2–15.9
Average weight, g	139.0	23.7	55.3–269.3
Number of species	3.9	0.4	2–6

min of leaving. When striking, the eagles entered the water feet first at a low angle and only took fish that were at or just below the surface.

We watched eagles for 669.5 h observer-time and 1030.98 h eagle-time, including 490.25 h (47.6%) male eagle-time, 526.0 h (51.0%) female eagle-time, and 14.73 h (1.4%) immature eagle-time. We recorded 67 occurrences of eagles obtaining fish, including 60 (89.6%) occasions when they captured fish in open water, 3 (4.4%) when they scavenged dead fish from the shoreline, and 4 (6.0%) when they stole fish from Black Kites. We also recorded 32 occurrences of eagles eating fish or delivering fish to their mates when we did not see an eagle obtain the fish. On one occasion we observed an eagle eating a domestic duckling (*Anas* sp.). We did not see the eagle capture the duckling, but the local people claimed that the same eagle pair had killed domestic ducklings and turkey (*Meleagris* sp.) poults at the same lake on several occasions in 1996.

Of the 67 occasions when we saw eagles obtain fish, the eagles were adult males on 53 (79.1%) occasions, adult females on 13 (19.4%), and an immature on 1 (1.5%) occasion. Nine (69.2%) of 13 adult females that we saw capture fish were not nesting at the time. The other four (31.8%) were incubating eggs. All 32 occasions on which we saw eagles eating or delivering fish but did not see them catch the fish involved adult male eagles. All four instances of piracy from kites occurred at the same lake and involved two cooperating adult male eagles associated with the same territory. In each case, the eagles harassed a kite until it dropped its fish, which one of the eagles then retrieved.

Foraging rates and fish abundance.—Male fish-eagle kills/search was positively correlated with number of fish species caught in gill nets ($\rho = 0.909$, $P < 0.001$). There were no other significant correlations between fish-eagle foraging rates (Table 2) and fish variables (Table 3). We only analyzed male foraging because we rarely saw females forage.

The Madagascar Fish-Eagle search rate peaked in the early morning and again, at a higher level, in the early afternoon (Fig. 1A). Foraging success, expressed as the proportion of prey searches that resulted in kills, was highest before 10:00 and after 16:00 but lower between these times (Fig. 1B).

Dietary preference.—Of the 99 observed occurrences of fish-eagles capturing, carrying, or eating fish, we were able to identify 68 (68.7%) either to species or to a closely related group of species (Table 4). We were unable to identify eagle-caught tilapia to species or to distinguish between the closely related *Oreochromis* and *Tilapia* genera. In our gill net samples, we caught 271 fish of 12 species, including four species of tilapia and eight other species. The total weight of the catch at all nine lakes was 41.1 kg.

We combined all native fish species into a single group because our catches of each species were too small to analyze separately (Table 4). The proportions of fish species differed significantly between the fish-eagle catch and the gill net catch ($\chi^2 = 41.97$, df = 4, $P = 0.001$). The 95% confidence limits for the difference between the proportion used and the proportion available suggested that fish-eagles catch *Ophicephalus striatus* in greater proportion, *Cyprinus carpio* in lesser proportion, and tilapia, *Heterotis niloticus*, and native species in equal proportion to their relative abundance.

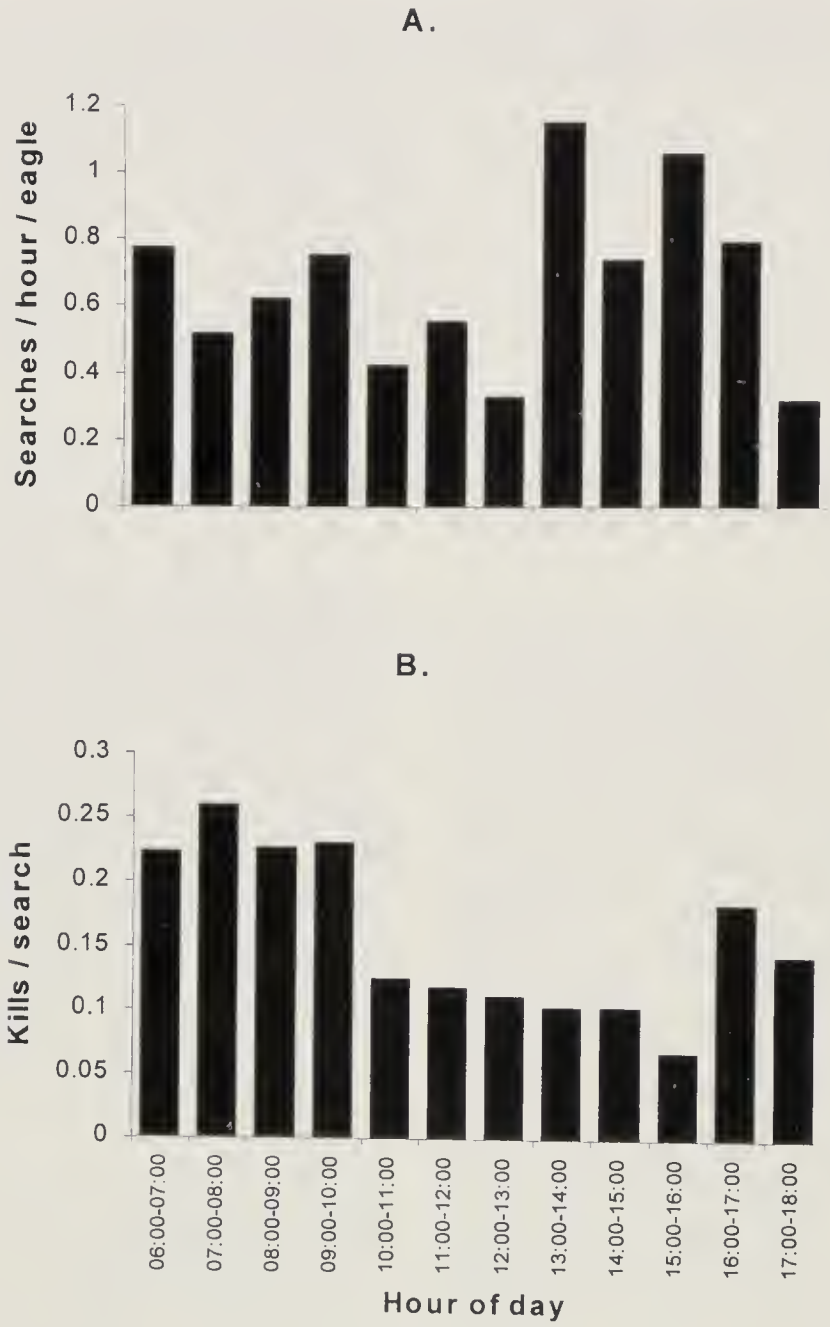

FIG. 1. Madagascar Fish-Eagle prey searches per hour per eagle (A) and prey searches resulting in kills (B) by time of day at nine lakes in western Madagascar, May–August, 1996.

DISCUSSION

Foraging behavior.—Our observation that 4.4% of fish taken by Madagascar Fish-Eagles were scavenged was lower than scavenging rates that Mersmann (1989) and Brown (1993) reported for Bald Eagles (25% and 7.7%, respectively) but comparable to the 4% reported by Stalmaster and Plettner (1992). We did not see fish-eagles take floating dead fish from the surface in open water, but it is possible that some of the fish that we observed eagles catch from a distance were dead fish floating below the water surface.

We are unaware of previous reports of piracy or capture of avian prey by the Madagascar Fish-Eagle. It is unclear why we observed four instances of piracy at one of the lakes and none at the other eight lakes. We saw numerous other fish-eating birds at all the lakes, including Black Kites, herons, storks, anhingas, and cormorants.

Although we observed adult male eagles incubating eggs and tending nestlings, it appears that the male does most of the foraging for the pair, at least during early nesting. The four instances in which we observed incubating females catch fish occurred near the nest when males were not present. The most advanced

TABLE 4. Fish caught (number and % of total) and number of lakes where fish were caught (out of nine) by Madagascar Fish-Eagles and in gill nets in western Madagascar, May–August, 1996.

Fish species[a], family	Fish-eagle catch			Gill net catch		
	No. of fish	% of fish	No. of lakes	No. of fish	% of fish	No. of lakes[b]
Exotic						
Tilapia[c], Cichlidae	44	64.7	9	183	67.5	9
Heterotis niloticus, Osteoglossidae	7	10.3	3	17	6.3	3
Cyprinus carpio, Cyprinidae	2	2.9	2	33	12.2	1 (2)
Ophicephalus striatus, Channidae	10	14.7	6	1	0.4	1 (6)
Native						
Megalops cyprinoides, Megalopidae	2	2.9	2	18	6.6	6 (1)
Arius madagascariensis, Ariidae	3	4.4	3	14	5.2	5
Glossogobius giuris, Gobiidae	0	0	0	2	0.7	1
Ambassis gymnocephalus, Ambassidae	0	0	0	2	0.7	1
Scatophagus tetracanthus, Scatophagidae	0	0	0	1	0.4	1
TOTAL	68	100		271	100	

[a] Unidentified fish that fish-eagles caught (n = 31) were excluded.

[b] Number in parentheses represents additional lakes where each fish species was known to be present either from 1995 gill net sampling or from fish catches of local fishermen.

[c] Tilapia species included in order of decreasing gill net catch: *Oreochromis macrochir*, *Tilapia zilii*, *O. mossambicus*, and *O. niloticus*.

nesting attempt we observed had a 2–3 week old downy chick, so we were unable to document whether female fish-eagle foraging rates change as nesting progresses.

Foraging rates and fish abundance.—The strong positive correlation between fish-eagle kills/search and number of fish species may indicate that the eagles forage most effectively at lakes that have the highest fish species diversity. In a previous study, Berkelman (1997) found that fish species diversity, along with shoreline perch density, was one of the best predictors of fish-eagle lake use, lending further support to the importance of fish species diversity. However, the strength of the correlation between foraging success and fish species diversity may be related to the low range of variability in number of fish species caught (2 to 6) at lakes in this study.

The early morning peak in search rate that we observed also was reported for Madagascar Fish-Eagles by Razafindramanana (1995) and for Bald Eagles (Steenhof et al. 1980, Mersmann 1989) and Ospreys (*Pandion haliaetus*; Flemming and Smith 1990). This peak may result from hunger after fasting overnight or from eagles taking advantage of greater fish availability and calmer weather during the early morning hours. The early afternoon search rate peak may reflect eagles that have digested the morning food and are hungry again. Whitfield and Blaber (1978) observed a midday foraging peak in African Fish-Eagles (*Haliaeetus vocifer*) and suggested that the eagles were taking advantage of thermals at this time, but the Madagascar Fish-Eagles that we observed foraged mostly low over the water from a perch. Daily weather patterns varied little during the study, so differences among eagle pairs in foraging rates and success probably were not related to weather.

Dietary preference.—The results suggest that Madagascar Fish-Eagles prefer *Ophicephalus striatus* to other fish and avoid *Cyprinus carpio*. *Ophicephalus striatus* was the largest fish species that we saw fish-eagles capture. We estimated the largest ones caught by fish-eagles to be between 1 and 1.5 kg. This species is a predatory fish that was introduced to Madagascar in 1978 (Reinthal and Stiassny 1991). In field experiments, Bald Eagles selected large fish more often than smaller fish during the breeding season, but not during the non-breeding season (Jenkins and Jackman 1995); Madagascar Fish-Eagle preference for *O. striatus* may reflect the eagle's greater energy requirements during the breeding season. Fish-eagles showed no preference for *Heterotis niloticus*, another large introduced fish species, but it was present in only three (33.3%) of the nine lakes. *Cyprinus carpio* may not be used because this species feeds on the bottom of lakes (Scott and Crossman 1973) where it is difficult for eagles to catch.

The results also may indicate biases in the fish abundance data. *Ophicephalus striatus,* a visually orienting predator, may be better at avoiding entanglement in gill nets than the other fish species. All of the *C. carpio* abundance data were from a single lake where we caught 33 individuals. This lake was so shallow (0.9 m) that both gill nets extended to the bottom and consequently were more likely to catch bottom-dwelling fish such as *C. carpio.*

The use and relative abundance data for tilapia, the most abundant fish in all of the lakes, were similar (64.7% of identifiable fish-eagle catch and 67.5% of gill net catch). Tilapia were introduced to Madagascar for aquaculture in the 1950s (Kiener 1963) and have since spread to most bodies of freshwater throughout the island. The predominance of tilapia in the fish-eagles' diet in this study suggests that the Madagascar Fish-Eagle is an opportunistic predator that catches whatever prey species are most abundant. Thus, the marked change in species composition of Madagascar's freshwater fish fauna resulting from exotic species introductions (Loiselle 1993, Reinthal et al. 1995) probably has not been detrimental to the island's fish-eagle population. The positive relationship between fish-eagle foraging success and number of fish species suggests that the fish-eagle population may be sensitive to declines in fish species diversity.

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THE RELATIONSHIP BETWEEN SPOTTED OWL DIET AND REPRODUCTIVE SUCCESS IN THE SAN BERNARDINO MOUNTAINS, CALIFORNIA

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ABSTRACT.—We analyzed the breeding season diets of California Spotted Owls (*Strix occidentalis occidentalis*) in the San Bernardino Mountains from 1987 through 1991 to estimate the relative importance of individual prey species to owl reproduction. We identified a total of 8441 prey remains from 109 unique territories, which represents the largest collection of prey remains from a single Spotted Owl population. Dusky-footed woodrats (*Neotoma fuscipes*) and Jerusalem crickets (*Stenopelmatus fuscus*) were the most frequently consumed taxa (42.2% and 20.7%, respectively), but dusky-footed woodrats dominated Spotted Owl diets by biomass (74.0%). Spotted owls consumed primarily mammals by both frequency (66.4%) and biomass (95.3%). After excluding territories with less than 20 prey remains, we compared the diets of 24 nonnesting, 24 unsuccessfully nesting, and 58 successfully nesting pairs of Spotted Owls from 56 unique territories; estimated diet along a large elevational gradient; and controlled for interterritorial and annual variation in diet. A significant relationship existed between reproductive status and the percent biomass of woodrats in Spotted Owl diets where successful nesters consumed a greater percent biomass of woodrats ($\bar{x}$ = 81.8) than nonnesters ($\bar{x}$ = 74.1) but not unsuccessful nesters ($\bar{x}$ = 75.5). Unsuccessful nesters and nonnesters did not consume a significantly different percent biomass of woodrats. The percentage of woodrat biomass in Spotted Owl diets increased with elevation but did not differ among territories or years. We hypothesized that breeding Spotted Owls were able to meet the increased energetic demands associated with producing young by consuming primarily large, energetically profitable prey such as woodrats. *Received 6 May 1998, accepted 21 Oct. 1998.*

The Spotted Owl (*Strix occidentalis*) preys on a wide range of vertebrate and invertebrate taxa, but primarily on a few species of small mammals (Gutiérrez et al. 1995). The distribution of these small mammals has an important influence on the owl's home range size (Carey et al. 1992, Zabel et al. 1995), habitat use patterns (Carey et al. 1992, Carey and Peeler 1995, Zabel et al. 1995, Ward et al. 1998), and demographic rates (Franklin 1997, Ward et al. 1998). In particular, prey abundance positively influences Spotted Owl reproduction. Ward and coworkers (1998) found that dusky-footed woodrats (*Neotoma fuscipes*) were more abundant in the territories of breeding Northern Spotted Owls (*S. o. caurina*) than in the territories of nonbreeding owls. Although this difference was not statistically significant, the authors suggested that high variation in woodrat abundances resulted in low statistical power for rejecting the hypothesis of no difference between breeders and nonbreeders. Franklin (1997) showed that the distribution of woodrat habitat explained a large amount of interterritorial variation in Northern Spotted Owl reproductive success. In addition, studies of other strigids demonstrate convincingly that reproduction for most owl species is limited, at least in part, by prey availability (see Verner et al. 1992 for a review).

Assuming that Spotted Owl reproductive success is determined in part by food availability, food habit studies based on prey remains from egested pellets can be used to examine the relative importance of individual prey species for reproduction. Such studies have shown that successful breeders consume a greater proportion of large prey than unsuccessful breeders (Barrows 1985, 1987; Thrailkill and Bias 1989; White 1996), although Ward and coworkers (1998) found no difference. These studies have been based upon relatively few prey items or owl territories which has resulted in (1) data being pooled among territories or (2) data from a

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particular territory being considered independent from year to year. The first approach weights all territories equally regardless of the number of prey items collected. For example, a breeding territory from which one prey item was collected is given the same weight as a breeding territory with hundreds of prey items. The second approach results in pseudoreplication and can dramatically inflate the probability of rejecting the null hypothesis (Hurlbert 1984) that breeding and nonbreeding Spotted Owls have the same diets. This is especially likely because Spotted Owl diets exhibit interterritorial variation (Laymon 1988).

Because previous diet studies were based on relatively few territories sampled from large, open populations, inferences about the relationship between diet patterns and the breeding ecology of the Spotted Owl are limited. We have been studying the entire population of California Spotted Owls (*S. o. occidentalis*) in the San Bernardino Mountains of southern California since 1987. It is the largest subpopulation within the southern California owl metapopulation (Noon and McKelvey 1992, LaHaye et al. 1994) and occupies a diverse array of habitats along a large elevation gradient. This allowed us to estimate diet over a range of ecological conditions and reliably evaluate its relationship with reproduction. In this paper we compare the diets of nonnesting, unsuccessfully nesting, and successfully nesting Spotted Owls throughout the breeding season (March through October), enumerate the food habits of individuals of this population, and compare our results to other food habit studies of the California Spotted Owl.

STUDY AREA AND METHODS

The San Bernardino Mountains Study Area was located approximately 140 km east of Los Angeles, California and encompassed 1890 km^2 with elevations ranging from 800–3500 m. Mean annual precipitation ranged from less than 20 cm to more than 100 cm and was strongly influenced by elevation and topography (Minnich 1988). The vegetation was diverse, ranging from Mojave Desert scrub (Vasek and Barbour 1988) at lower elevations to alpine (Major and Taylor 1988) on San Gorgonio Mountain. Most Spotted Owls occupied conifer dominated forest (Sawyer et al. 1988, Thorne 1988) between 1000 m and 2500 m elevation.

Owl survey methods.—We surveyed the study area for Spotted Owls following methods described by Franklin and coworkers (1996) during the breeding season (March–October), 1987–1991. We conducted 1113 nocturnal surveys during which we spent 15 min at an individual point or walked along designated routes, using vocal imitations of Spotted Owl calls to survey the forested habitat within the study area. Survey points and routes were placed so that all of this potentially suitable habitat was surveyed each year. We conducted 1659 diurnal surveys at territories that were known to be occupied in order to locate nests, locate roosts, collect regurgitated pellets, and assess reproductive status. We conducted initial diurnal surveys for each territory in March or April and conducted follow-up diurnal surveys every 3 to 5 weeks. We collected pellets by thoroughly searching areas underneath Spotted Owl nests and roosts during most diurnal surveys. We assessed nesting status by feeding owls live mice (*Mus musculus*) during diurnal surveys (Franklin et al. 1996). We considered an owl pair not to have nested if one member of the pair ate or cached four consecutive mice during a single diurnal survey prior to 31 May. Although only one formal survey was conducted to assess nesting status, multiple surveys were conducted at each territory to band and resight owls. If a nest was located during one of these surveys, the owls at that particular territory were of course considered to be nesting. When a nest was located, we used the same method to locate fledglings or to determine nest failure. Owls that did not take sufficient mice were not included in the study.

Quantifying Spotted Owl diets.—We dissected all collected pellets and isolated all identifiable prey remains. Identifiable remains included skulls (birds and mammals), mandibles (mammals, reptiles, and invertebrates), legs (birds and invertebrates), claws (invertebrates), and bills (birds). Remains collected during each diurnal survey were enumerated to the lowest possible taxonomic level, and the highest count was taken as the total number of prey items for that survey. If, for example, pellets collected during a single survey contained one woodrat skull, two left mandibles, and three right mandibles, three woodrats were considered to be present. The percent frequency of each taxa (Marti 1987) was then calculated for each territory pooled among years. The percent biomass (Marti 1987) was calculated for each territory using the mean prey weights in Table 1. The mean percent frequency and biomass among territories were used as estimates of the overall diet composition. This approach weights all territories equally so that overall percentages were not biased towards territories with many prey remains (Swanson et al. 1974).

Statistical analyses.—Statistical analyses were performed only on the biomass data 1988–1991 because of small sample sizes in 1987 and because we felt biomass more accurately represented the energetic importance of each prey taxa.

We used a mixed-model ANOVA approach (Proc MIXED of pc SAS, version 6.12; Littel et al. 1996) to estimate variation in Spotted Owl diet, where each diet variable was considered as the dependent variable in a separate model. We treated reproductive status (non-

TABLE 1. Diet of Spotted Owls in the San Bernardino Mountains, California.

	Mean prey weight (g)	Source[a]	% of prey by frequency (n = 8,169)	% of prey by biomass (707,193 g)
Mammals				
Neotoma fuscipes	173.7	1	42.2	74.0
Thomomys bottae	124.4	1	7.4	10.4
Glaucomys sabrinus	121.5	2	2.1	3.0
Peromyscus spp.	22.1	1	11.3	4.0
Microtus spp.	60.2	1,2	1.8	1.3
Sylvilagus spp.	538.3	2	0.2	1.0
Sciurus griseus	785.0	2	0.1	1.0
Dipodomys merriami	42.1	2	0.1	<0.1
Scapanus latimanus	55.2	2	0.4	0.3
Spermophilus lateralis	153.4	1	0.1	0.2
Tamius merriami	67.6	1,2	0.1	0.1
Antrozous pallidus	21.5	2	<0.1	<0.1
Eptesicus fuscus	14.0	2	<0.1	<0.1
Lasiurius cinereus	25.5	2	0.1	<0.1
Myotis spp.	4.9	2	0.1	<0.1
Perognathus spp.	14.4	1	0.1	<0.1
Sorex ornatus	5.1	2	0.5	<0.1
Subtotal			66.4	95.3
Birds	64.4	3	4.3	3.5
Invertebrates				
Stenopelmatus fuscus	2.0	4	20.7	0.9
Prionus californicus	2.0	3	3.6	0.1
Scorpionida	2.0	4	2.7	0.1
Unidentified	2.0	4	2.1	0.1
Subtotal			29.1	1.2
Reptiles				
Sceloporus spp.	10.0	3	0.1	<0.1

[a] Sources were (1) specimens from the San Bernardino Mountains in the Museum of Vertebrate Zoology at University of California, Berkeley collections, (2) specimens from nearest available location to the San Bernardino Mountains in the Museum of Vertebrate Zoology at University of California, Berkeley collections, (3) Forsman et al. (1984; biomass of birds divided by the number of birds in tables 12–14), (4) estimated based on prey size.

nesters, unsuccessful nesters, and successful nesters) and year as fixed effects, and elevation (at the center of activity for each territory) as a covariate. We used territory as a random blocking factor to estimate variation in diet among territories and control for nonindependence of samples within territories. Two-way interactions between reproductive status and the other main effects were included in the model. Main effect by territory interactions were assumed to be nonexistent which resulted in all effects being tested over the residual mean square (Newman et al. 1997). Significant fixed effects were further tested with t-tests on least squares means using sequential Bonferonni adjustments on critical values (Rice 1989). This procedure involves testing each comparison, starting with the most significant and stopping at the first nonsignificant comparison, using $\alpha/(1 + k - i)$ as the critical value where k is the number of post-hoc comparisons and i is the number of the comparison.

Proper use of an ANOVA model requires a normally distributed dependent variable and equality of variances among treatment levels (Zar 1984). Because the percent biomass of woodrats was a proportional variable, and hence formed a binomial distribution, we used the square root-aresine transformation to normalize the data (Zar 1984). Normality was then tested with the Shapiro-Wilk statistic (Zar 1984). Equality of variances among reproductive groups was tested with an F-test (Zar 1984).

By using diet as the dependent variable we do not imply that diet is a function of reproductive status; the mixed modeling approach simply provides a convenient way of examining variation in diet in relation to other variables (including reproduction). We believe that this approach is justified because (1) the goal of the study was to determine if diet differed among nonnesting, unsuccessfully nesting, and successfully nesting Spotted Owls, and (2) it is appropriate to analyze a correlative relationship with a linear model because the resultant F-statistic provides a test of the null hypothesis that the multiple correlation coefficient R is zero (Zar 1984).

RESULTS

Spotted Owl diets.—We identified a total of 8441 prey items from 109 unique Spotted Owl

TABLE 2. The effect of reproductive status, elevation, and year on the percent biomass of woodrats in Spotted Owl diets in the San Bernardino Mountains. Results are from a mixed-model ANOVA (Littel et al. 1996) where reproductive status and year were fixed effects, elevation was a covariate, and territory[a] was a random blocking factor effect.

Effect	ndf	ddf	*F*	*P*
Reproductive status	2	36	3.65	0.04
Elevation	1	36	34.93	<0.01
Year	3	36	1.87	0.15
Reproductive status*year	3	36	1.17	0.35
Reproductive status*elevation	1	36	3.16	0.06

[a] Territory was not significant ($Z = 1.43$, $P = 0.15$).

territories. This represents, to the best of our knowledge, the largest collection of prey items recorded from a single Spotted Owl population. When estimating the overall diet composition, we excluded territories from which fewer than 20 prey remains were collected during the entire study period (this resulted in a subsample of 8,169 prey remains from 71 territories). Dusky-footed woodrats and Jerusalem crickets (*Stenopelmatus fuscus*) were the most common taxa by frequency (42.2% and 20.7%, respectively). White-footed mice (*Peromyscus* spp.) and northern pocket gophers (*Thomomys bottae*) were less common by frequency (11.3% and 7.4%, respectively). No other taxa contributed more than 4.3% to the total number of prey items (Table 1).

Dusky-footed woodrats dominated Spotted Owl diet by biomass (74.0%), followed by pocket gophers (10.4%). Dusky-footed woodrats were the largest (173.7 g) of the common prey items. Western grey squirrels (*Sciurus griseus*) and cottontails (*Sylvilagus* spp.) were larger, but represented only 2.0% of the total biomass. No other taxa contributed more than 4.0% to the total biomass consumed (Table 1). Mammals contributed 66.4% and 95.3% to the total number of prey items and the total biomass, respectively. Invertebrates contributed 29.1% to the total number of prey items, but only 1.2% to the total biomass.

Variation in Spotted Owl diets.—For statistical analyses, we excluded territories represented by fewer than 20 prey items in any one year. In doing so, we retained a large sample size (106 samples from 56 unique Spotted Owl territories; 24 nonnesters, 24 unsuccessful nesters, and 58 successful nesters) and were able to estimate the percent biomass of woodrats with reasonable precision on a territory by territory basis (mean CV = 0.08, maximum CV = 0.27). The percent biomass of pocket gophers was estimated with considerably less precision (mean CV = 0.50, maximum CV = 1.00). In addition, the percent biomass of pocket gophers was highly and negatively correlated with the percent biomass of woodrats ($r = -0.67$, $P < 0.01$, $n = 106$). For these reasons, we did not model the percent biomass of pocket gophers statistically.

Although the percent biomass of woodrats was not distributed normally ($W = 0.93$, $P < 0.01$) the variance in the percent biomass of woodrats did not differ between the least variable (successful nesters) and the most variable (unsuccessful nesters) reproductive groups ($F_{23,57} = 1.46$, $P > 0.05$). Because ANOVA is sensitive to heterogeneity of variances among treatment levels but robust to departures from normality (Hicks 1993), we assumed the data met the assumptions of the model.

A significant relationship existed between reproductive status and the percent biomass of woodrats in Spotted Owl diets (Table 2). Successful nesters consumed a greater percent biomass of woodrats ($\bar{x} = 81.8 \pm 1.5$ SE) than nonnesters ($\bar{x} = 74.1 \pm 2.4$; $t_{0.017,36} = 2.49$, $P = 0.017$) but not unsuccessful nesters ($\bar{x} = 75.5 \pm 2.4$; $t_{0.025,36} = 2.08$, $P = 0.044$), although the difference between successful and unsuccessful nesters was nearly significant. Unsuccessful nesters and nonnesters did not consume a different percent biomass of woodrats ($t_{0.050,36} = 0.04$, $P > 0.05$). The percentage of woodrat biomass in Spotted Owl diets did not differ among territories but increased with elevation (Table 2; Fig. 1). The interaction between elevation and reproductive status was

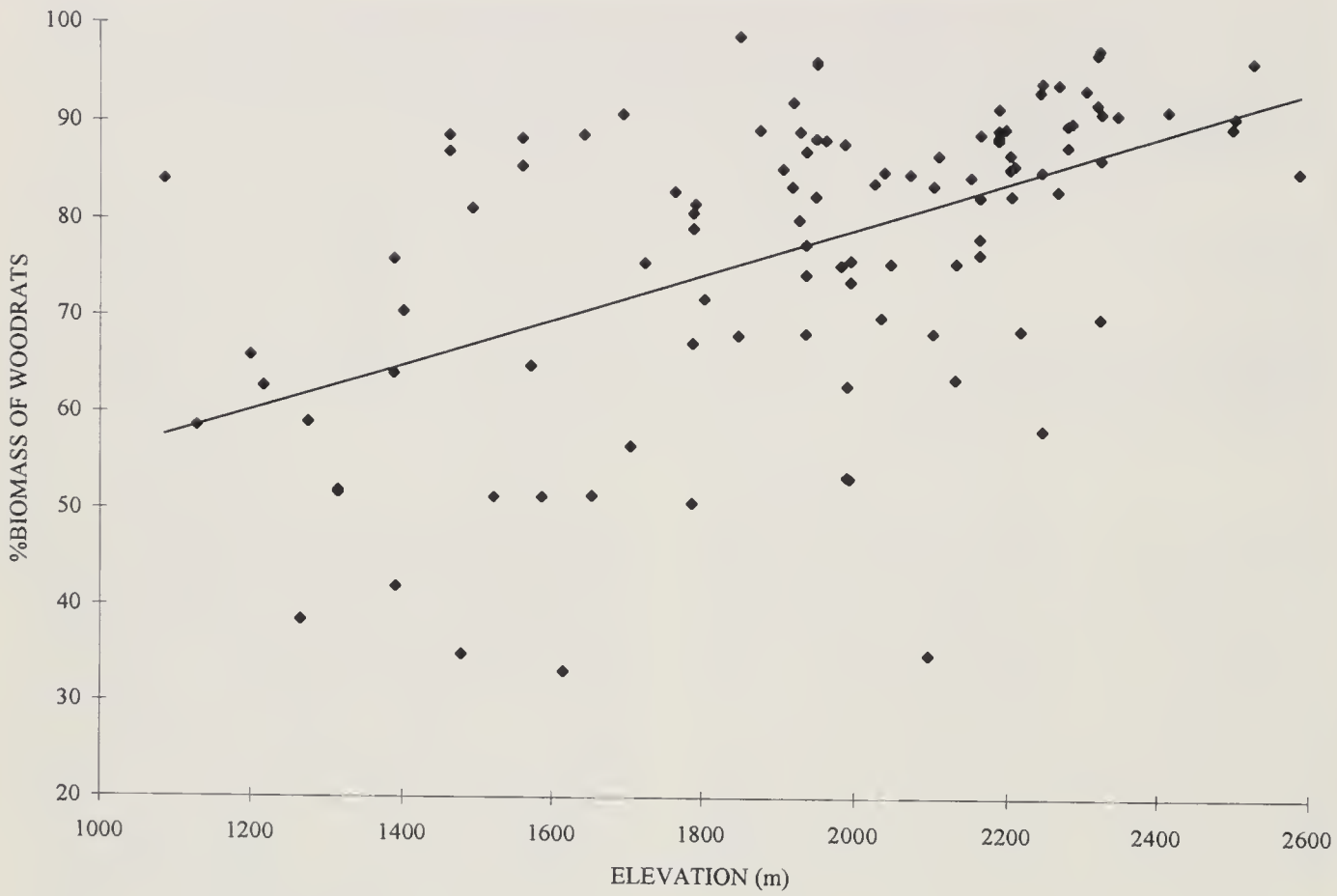

FIG. 1. The relationship between elevation and the percent biomass of woodrats in the diets of Spotted Owls in the San Bernardino Mountains, California, 1988–1991 ($b = 0.000085$, $R^2 = 0.26$, df = 104, $P < 0.01$).

not significant (Table 2), indicating that the percent biomass of woodrats increased with elevation at a constant rate for nonnesters, unsuccessful nesters, and successful nesters. The percentage of woodrat biomass in the owl's diet did not differ among years and no interaction existed between year and reproductive status (Table 2).

DISCUSSION

For an owl pair to produce young, females must acquire sufficient fat reserves prior to nesting, and males need to provide sufficient amounts of food to the female and nestlings during the nesting period (Hirons 1985). Dusky-footed woodrats are relatively large and may have provided an energetically profitable food source that enabled Spotted Owls to reproduce successfully. This idea is supported by Ward and coworkers (1998) who showed that selection of dusky-footed woodrats provided an indirect benefit to Spotted Owl fitness by reducing the amount of habitat needed to reproduce successfully. Further, Orians and Pearson (1979) predict that central place foragers such as Spotted Owls (Carey and Peeler 1995) can increase the rate of energy return to the central place (nest), and hence fitness, by consuming large prey. By consuming large prey, the male can minimize the number of flights from the point of capture to the nest, allowing more time for hunting.

Since the diet of unsuccessful nesters was more similar to nonnesters than successful nesters, consuming woodrats may be more important for incubation and brooding than for nest initiation. This is supported by the fact that the energetic cost of egg production is relatively small compared to the amount of energy needed to provision the female and young during the nesting period (Ward et al. 1998).

Our results support Barrows (1985, 1987), Thrailkill and Bias (1989), and White (1996) who found that Spotted Owls that fledged young consumed a higher proportion of large prey than Spotted Owls that did not fledge young. Despite the sample size limitations of these previous studies, it appears that a true difference in diet, particularly in terms of prey

size, exists between breeding and nonbreeding Spotted Owls. The importance of prey size has also been observed for Black-shouldered Kite (*Elanus caeruleus*; Slotow and Perrin 1992) and Common Kestrel (*Falco tinnunculus*; Korpimäki 1986) reproduction, suggesting that this may be a common pattern for raptorial species.

It is possible that the difference between successful nesters and nonnesters was statistically significant, but not biologically significant. An 8% difference in the percent biomass of woodrats is relatively small when compared to the additional amount of food a male must procure to provision a female and even just one nestling. Based upon Ward's and coworkers' (1998) energetic calculations, a male must increase the amount of food he procures by 276% in order to provision the female and a juvenile from egglaying to fledging. However, the dietary difference observed between breeders and nonbreeders may be only one of the factors that allows an owl pair to produce young. For example, the variation in diet caused by breeding status may simply reflect higher prey availabilities in the territories of breeding and nonbreeding owls (see below).

The percent biomasses of the prey species presented here are not necessarily estimates of the total amount of prey taken because it is unlikely that we collected all regurgitated pellets. Hence we cannot evaluate the effect of food supply on reproduction. It is possible that even though successfully nesting owls consumed a greater percent biomass of woodrats, they obtained less total biomass from woodrats than nonnesters or unsuccessful nesters. However, this seems unlikely because breeding Spotted Owls need to take considerably more total prey to feed their juveniles.

Without measuring prey abundances, we cannot be certain if the relationship between Spotted Owl diet and reproduction was the result of differences in prey availability or prey selection among territories. Spotted Owls select dusky-footed woodrats more than would be expected based on availability in both northern and southern California (Hedlund 1996, Ward et al. 1998). Further, Barrows (1987) found that Spotted Owl pairs shift from large to small prey after nest failure and suggested that this change in prey selection was in response to reduced energy requirements. If Barrow's hypothesis was true for our population, unsuccessful nesters should have had an intermediate percentage of woodrat biomass in their diets. Since this did not occur, we consider it more likely that the difference in the percent biomass of woodrats between owls that fledged young and owls that did not fledge young was the result of differences in prey availability among territories. Optimal foraging theory (see Pyke et al. 1977 for a review) predicts, and raptor field studies show (Korpimäki 1986, Steenhof and Kochert 1988), that when the density of primary prey is high within the landscape, the percentage of that prey in the predator's diet is also high (i.e., a functional response). Hence, if woodrats occurred at higher densities in the territories of successfully reproducing owls (Franklin 1997, Ward et al. 1998) one would expect these owls to consume a greater percentage of woodrats.

Bull and coworkers (1989) found that male Great Gray Owls (*S. nebulosa*) preferentially consumed small prey items at the point of capture and brought large prey items back to the nest. Although this presents a potential source of bias, we do not believe that it affects the conclusions of this study. For nesting owls, our pellets were probably biased towards males because we (1) often located male roosts and (2) females frequently flew away from the nest to egest pellets (personal observation). If Bull's and coworkers' (1989) findings are true for Spotted Owls, we may have underestimated the percent biomass of woodrats in the diets of nesting owls. This bias, however, would have decreased the difference between owls that fledged young and owls that did not fledge young.

Another potential bias is that pellets may not represent a random sample of the owl's diet. In particular, single prey-item Barn Owl (*Tyto alba*) pellets are more likely to contain large prey than expected by chance (Yom-Tov and Wool 1997). If this was true for our Spotted Owl population, the percent frequency and biomass of relatively large prey such as woodrats, pocket gophers, and northern flying squirrels (*Glaucomys sabrinus*) would be positively biased, while the percent frequency and biomass of relatively small prey such as white-footed mice would be negatively bi-

ased. However, these biases should be consistent for nonnesting, unsuccessfully nesting, and successfully nesting owls and should not affect the relationship between reproductive status and diet that we observed.

Although some similarities existed between Spotted Owl diets in the San Bernardino Mountains and other localities in southern California, some marked differences existed as well. For example, while the percent frequencies of woodrats and pocket gophers in Spotted Owl diets reported in this study were similar to those reported by Barrows (1980, 1987), white-footed mice comprised a considerably smaller percentage (11.3% versus 40.0%) and invertebrates a greater percentage (29.1% versus 18.0%) of the total prey items in this study. The percent biomasses of woodrats, pocket gophers, and most other prey taxa were remarkably similar to those reported by Barrows (1980, 1987).

In the Sierra Nevada, woodrats are the Spotted Owl's primary prey at low elevations but are almost completely replaced by flying squirrels at high elevations (Verner et al. 1992). In the San Bernardino Mountains, woodrats increased in Spotted Owl diets with elevation and flying squirrels were uncommon (2.1%). Flying squirrels are probably more abundant in the upper mixed-conifer and red fir (*Abies magnifica*) zones of the Sierra Nevada (see Waters and Zabel 1995) than they are in the San Bernardino Mountains where they reach the southern edge of their range (Hall and Kelson 1959). The San Bernardino Mountains apparently lack a relatively large alternative prey species at higher elevations and it is possible that most of the other prey species decrease in elevation as well. Woodrats are an important part of the Spotted Owl's diet in southern California, both in terms of biomass and reproduction, and we recommend that future management of forested habitat in this region promote high woodrat densities.

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FOOD, FORAGING, AND TIMING OF BREEDING OF THE BLACK SWIFT IN CALIFORNIA

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ABSTRACT.—The nestling diet and breeding seasonality of the Black Swift (*Cypseloides niger*) were studied in southern California 1990–1992. The peak (40%) of egg laying was in mid-June and the peak of fledging (60%) was mid- to late August (n = 87 nests). Winged ants comprised 91% (n = 1179 prey items, 10 boluses) of nestling diet. Three main prey size classes were found: 6, 8, and 13 mm. Food bolus mass increased and number of trips per day to feed the nestlings decreased with nestling age. The parents made short and long foraging trips during early morning hours and long trips from early to late afternoon. Short trips were observed only during the first half of the nestling period. During the last half of the nestling period, parent swifts made a single foraging trip per day that lasted about 12 hrs. Perhaps the short foraging bouts are for feeding the young, whereas the long foraging bouts are not only for feeding the young but also for parental energy storage. The single foraging bout, during the mid- and late nestling period, might also serve to store fat for migration by the adults. *Received 13 Feb. 1998; accepted 24 Oct. 1998.*

The Black Swift (*Cypseloides niger*) is a member of the subfamily Cypseloidinae which consists of 12–13 species, most of which are tropical or subtropical in their breeding distribution. The Black Swift is found locally in the West Indies, Middle America, and north through much of western North America to southeastern Alaska (Bent 1940; AOU 1957, 1983). For a species with such a wide latitudinal distribution, quantitative data on diet and timing of breeding are rare. Most of what is known about the Black Swift is limited to breeding and distributional records (e.g., Vrooman 1901, 1905; Michael 1927; Dixon 1935; Knorr 1961; Foerster 1987; Foerster and Collins 1990; Stiles and Negret 1994). This reflects the difficulty of studying this species because of its aerial life style and its usually inaccessible nest sites. Here I present new information on diet and timing of breeding of this species.

The Black Swift is a summer breeding visitor to western North America, and like many migratory species there, has a restricted breeding season. Furthermore, it has a proportionately large egg, a single-egg clutch, is single brooded, and has a long incubation and nestling period (Marín 1997). These factors should constrain variation in the timing of breeding of the Black Swift.

Swifts catch airborne insects and ballooning spiders (Lack and Owen 1955, Whitacre 1991). During the reproductive season, breeding cypseloidine swifts accumulate insects and arachnids in the back of the throat continuing into the esophagus and bind them with saliva to produce a sticky assortment of insects. This insect conglomerate or food bolus is produced exclusively to feed the nestling(s) and have never been reported outside the breeding season. Alive or dead these insects are complete, making them ideal for identifying and quantifying diets. Hespenheide (1975) pointed out that one difficulty in analyzing bird diets is knowing which is more important: the number or the size of food items. Some diet studies of New World swifts have addressed both parameters [e.g., Whitacre (1991)]; however, most have emphasized only one or they had small sample sizes (e.g., Collins and Landy 1968, Hespenheide 1975, Foerster 1987, Bull and Beckwith 1993, Marín and Stiles 1993). Other authors have considered only the number of prey items (e.g., Beebe 1949; Rathbun 1925; Rowley and Orr, 1962, 1965; Marín and Stiles 1992). One problem in quantifying swift diets is the source of prey samples, either stomach contents or food boluses. Stomach contents of adults are prey items that the adult bird has fed upon, whereas food boluses are prey fed to nestlings. Thus, examination of stomach contents versus food boluses might produce different results. Because my focus

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was on the diet of Black Swift nestlings, I analyzed only food boluses.

METHODS

Most data were gathered during a study of the breeding biology of the Black Swift in the San Jacinto Mountains, Riverside Co., California. The study site is at 1500 m elevation, and the surrounding area is montane forest. The study site was visited 40 times from 1990 to 1992, between the months of May and September. Observations were made in blocks of 4 to 7 hours, from 05:00 to 12:00, 12:00 to 19:00, or 19:00 to 23:00 PST, throughout the breeding season. For more detailed information on the study site and distribution of visits see Marín (1997) and references therein.

Data on nestling diet were obtained from regurgitated food boluses from adult swifts captured upon arrival at the nest. The boluses were weighed immediately (to nearest 0.1 g; Pesola scale) and placed in a vial containing alcohol. Insects in the boluses were counted and measured to the nearest 0.1 millimeter with a micrometer under a microscope in the lab.

Ten boluses (n = 1179 prey items) were collected from different adults on different dates and years throughout the study to minimize nest disturbance. Seven boluses were collected in 1991 and three during 1992. Bolus mass and time of collection were recorded for nine of them. I measured the length of 15 randomly selected individual prey items per prey species per bolus, and I used the average length as the mean of that species in the specific food bolus. Insects were sorted to morphospecies and identified to families using Borror and Delong (1970), Borror and White (1970), and Powell and Hogue (1979).

To assess timing of breeding, I combined field nest data (n = 20) with archived nest and egg data cards (n = 67; see Acknowledgments for list of sources), along with museum study skins and the literature. To determine length of the breeding season, I used egg laying, hatching, and fledgling periods. I restricted analyses of museum egg data cards to two areas in California: mountains (San Jacinto area) and coast (Santa Cruz Co.). I compared the estimated hatching date from the museum egg data cards to my own field data on hatching dates gathered at San Jacinto to look for potential date discrepancies between actual and estimated data. The incubation stage given in the egg data cards (e.g., fresh, commenced, advanced, etc.) was extrapolated using the known days of the incubation stage from San Jacinto (24 days; Marín 1997). I candled 16 eggs at San Jacinto and determined that no egg of this species could be blown without significantly damaging or destroying the shell by day 16–18. Thus, any museum egg specimen of this species was unlikely to have been collected beyond 18 days of incubation. I estimated the duration of each stage visible through candling as: "fresh" (0–4, 5 days) "veins and small embryo" (5–10 days), "embryo" (11–14 days), and "large embryo" (>15 days). These data were used to infer incubation stage (from the data cards) and to estimate egg laying dates. Using the known incubation and fledgling period (24 and 48 days, respectively; Marín 1997), the estimated laying, hatching, and fledging dates were compared and then combined with field data. The dates were separated by month, and each month was subdivided into early, middle, and late.

Rainfall data were gathered for each month for the years of study (1990–1992) and also 1963–1973 from the Idyllwild Fire Department weather station about 1.5 km from study area (National Oceanic and Atmospheric Administration 1991, 1992).

I was able to identify adults individually because they were already banded by C. Collins and K. Foerster because this was the main study site that Foerster (1987) used for his MS thesis work.

TABLE 1. Contents of food boluses (n = 10) of *Cypseloides niger* from San Jacinto, California.

Order	Family	Number
Isoptera		1
	Hodotermitidae	1
Hemiptera		27
	Pentatomidae	3
	Coreidae	10
	Miridae	2
	Reduviidae	11
	Nabidae	1
Homoptera		54
	Cicadidae	17
	Cicadellidae	36
	Aphidae	1
Neuroptera		8
	Hemerobiidae	1
	Myrmeleonitidae	3
	Corydalidae	1
	Family?	3
Coleoptera		1
	Buprestidae	1
Lepidoptera		3
	Pyralidae	1
	Family?	2
Diptera		
	Family?	11
Hymenoptera		1074
	Formicidae	1074
Arachnidea		1
TOTAL		1179

RESULTS

Nestling diet and foraging.—All boluses were composed of one predominant prey species, suggesting that the birds had fed on swarming species or highly localized prey. Winged ants were the majority of prey items (91%; Table 1). In 10 boluses the average proportion of female winged ants was 79.5 %

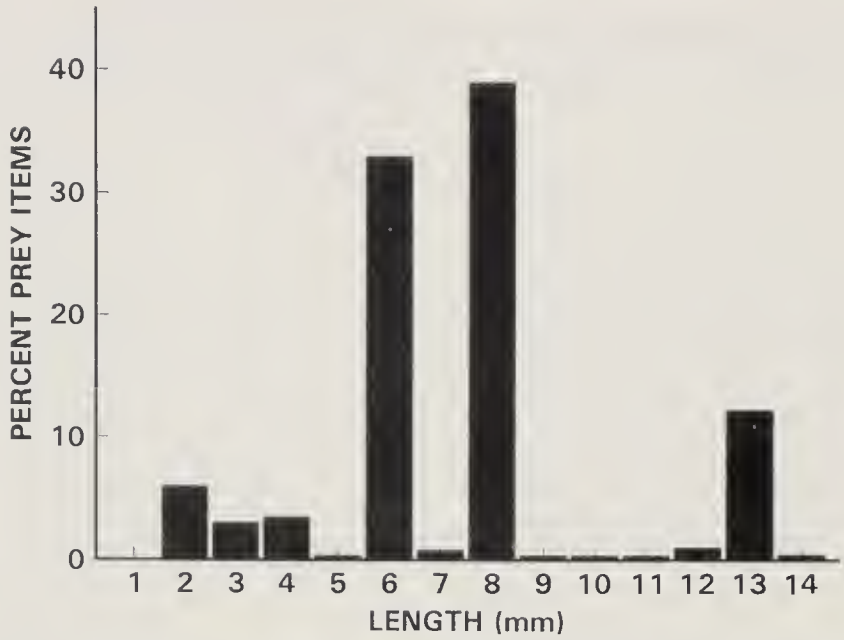

FIG. 1. Frequency distribution of prey sizes taken by the Black Swift (*Cypseloides niger*) in southern California. Data are from 10 food boluses (n = 1154 prey items); prey size categories are: 0.5–1.5 mm = 1; 1.6–2.5 mm = 2; 2.6–3.5 mm = 3; etc.

(range 20–100%; n = 1179 prey items). Sexual dimorphism in ants accounted for prey size differences among boluses. Male ants were smaller and ranged 2–6 mm, whereas females ranged 6–14 mm. Sometimes a bolus contained a small number of female ants but those ants were the largest prey. Thus, female winged ants had the highest volume/prey in all boluses. The average measurable prey size was 7.4 mm (range 1.8–14.5 mm; n = 1154). Three main size classes were found in the boluses: 6 mm (33%), 8 mm (39%), and 13 mm (12.2%; Fig. 1). Two length categories (6 and 8 mm) made up the bulk of the samples. Because only a few prey taxa were represented in the diet, size frequencies for all prey species follow a similar pattern.

Nestling age and bolus mass were positively correlated (r^2 = 0.93, $P < 0.001$, n = 10; Fig. 2). No correlation was found between mean prey size per bolus and chick age (r^2 = 0.08, $P > 0.05$) or mass per bolus (r^2 = 0.04, $P > 0.05$, n = 10). No individual prey item was weighed, but female winged ants were

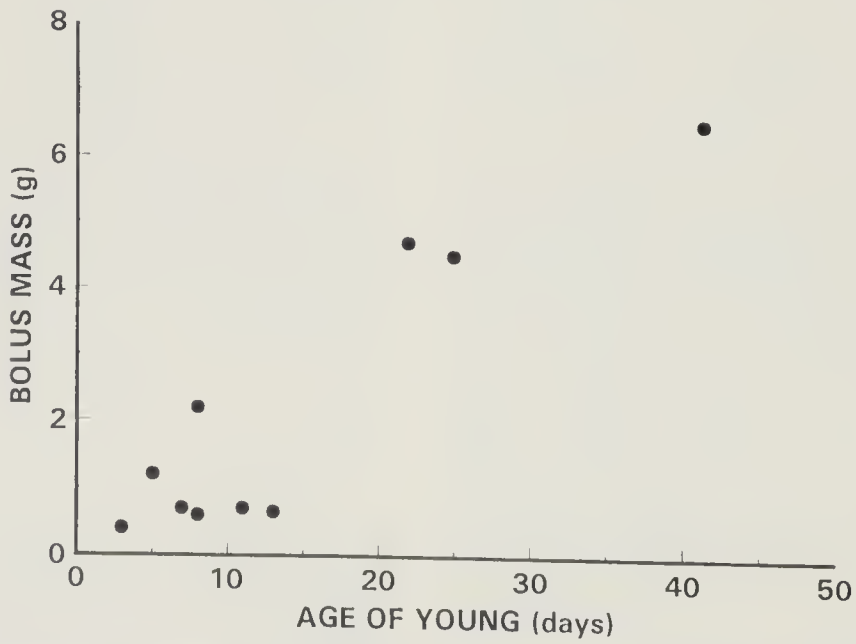

FIG. 2. Relationship between bolus mass and nestling age (r^2 = 0.93; $P < 0.001$, n = 10).

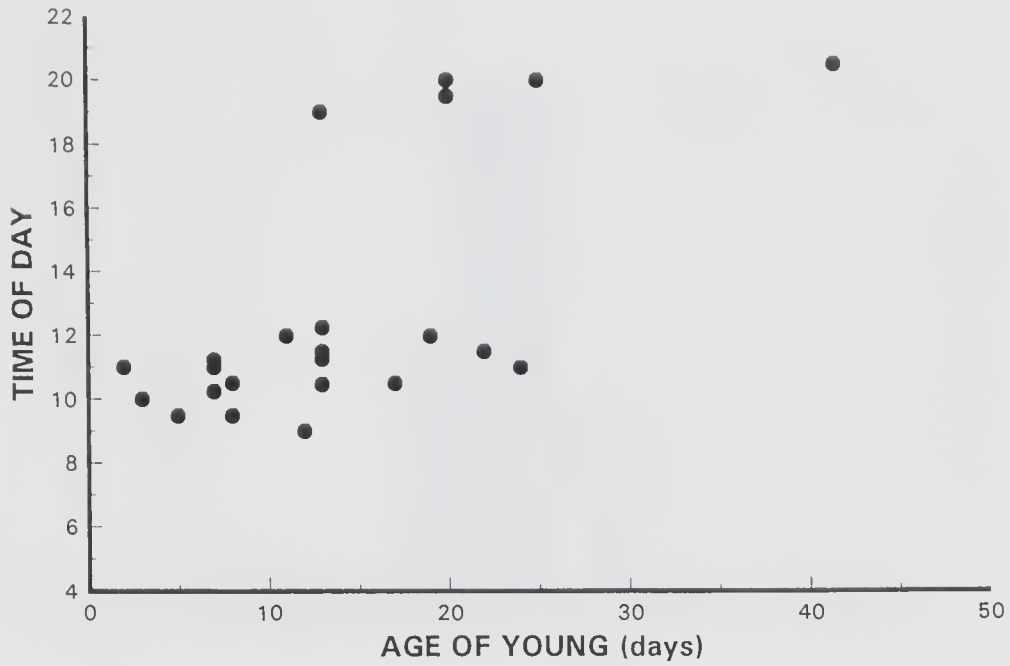

FIG. 3. Time of day young were fed versus their age. None of the adult birds were observed feeding young between the two feeding clusters or during early morning after 30 days.

undoubtedly the heaviest prey items because they were the largest. After day 30 I never saw any adults feed young in the morning; they were fed mainly late in the evening (Fig. 3). Other nestlings not included in the analysis because they were inaccessible and of unknown age, but at least 30 days old, were also observed being fed between 18:30–20:00. The overall pattern seems to be that as age increased, feeding rate decreased, but bolus mass increased (Figs. 2, 3).

Data gathered from adults feeding young at the nest showed two clusters of feeding times: between 8:30 and 12:30 and after 18:30 (Fig. 3). The birds usually left the cave at about 05:30. In two instances, however, some departed earlier unnoticed because of the darkness. This implies that they spent 3–7 hours searching for food for the first feeding bout. For the second bout, the birds were away from the nest longer: 6–8 hrs (Fig. 3). I never observed nestlings being fed between 12:30–18:30. I did not gather data late in the evening or at night during the early nestling stage so late arrivals and feeding at that stage are possible. If the intervals between feeding bouts were consistent through the season, then older nestlings often waited more than 12 hrs between meals when they were well grown or more than 30 days of age.

Breeding season.—Hatching dates were the main variable I used to compare the timing of breeding between a mountain site (San Jacinto area, San Bernardino Co., California) and a coastal site (Santa Cruz area, Santa Cruz Co., California). The San Jacinto data were primarily from my observations, whereas the Santa Cruz data were taken from museum nest and egg data cards. I found no significant difference between the coastal and mountain sites in timing of hatching (Fisher's exact Test (2-tail): $P > 0.05$). Therefore, I concluded that it was safe to pool both field and museum data for coastal and interior southern California. Most eggs were laid during mid-June (40%), with 30% during late June (Fig. 4). The earliest laying date was estimated to be 18 May, from an egg set collected in 1960 near Santa Cruz, California. The latest date for egg laying on the data cards was estimated to be 12 July 1921, from the same site as the earliest date. Some of the observed variation might be due to inter-year differences, which are difficult to evaluate with the present data. Nevertheless, most eggs (81%) had an estimated laying date in June. The earliest estimated date for hatching was about 11 June (same nest as above) and the latest date was about 5 August from the same site. In total, 89% of the hatching dates were in July; 24% of the estimated hatching dates were during the first 10 days of July and 53% during the middle third of

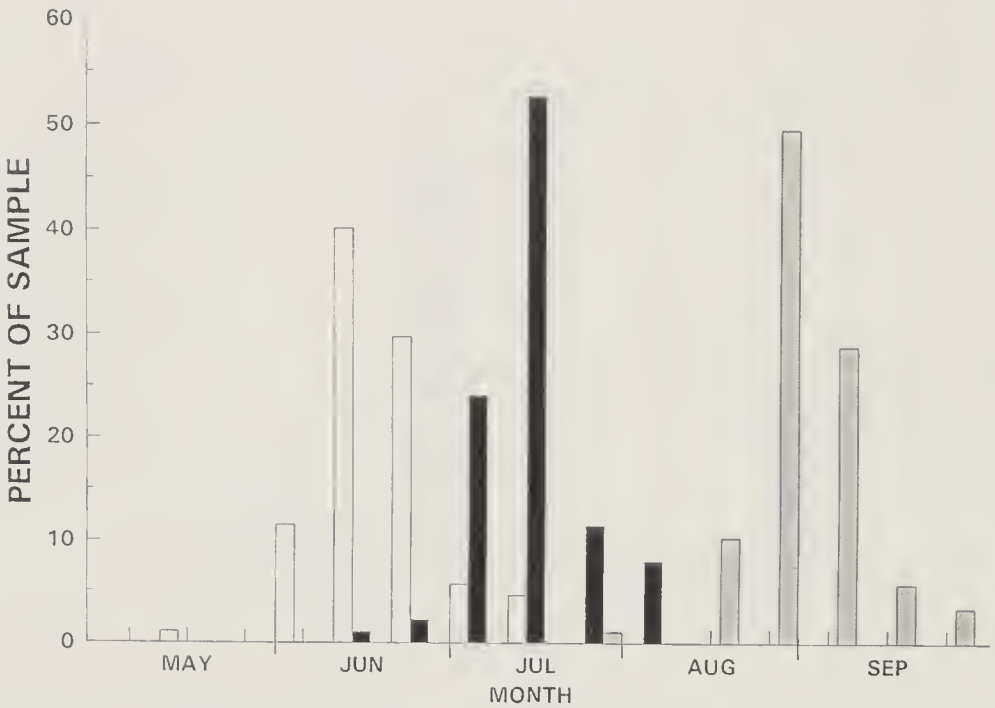

FIG. 4. Distribution of estimated dates of egg laying (open bars), hatching (black bars), and fledging (stipled on bars) of Black Swifts in southern California.

July. Sixty percent of the young were estimated to fledge during mid- to late August and 29% during the first 10 days of September. The highest proportion of fledging (78%) was estimated to occur between late August and early September (Fig. 4).

DISCUSSION

Contrary to most, if not all tropical cypseloidines, the southern California populations of the Black Swift breeds during the dry season. For the small, tropical cypseloidine swifts, rainfall itself can be as important a stimulus as food in initiating breeding. Moisture is needed to keep the appropriate conditions for nest "growth" and maintenance (Marín and Stiles 1992). Many Black Swifts did not build a nest at all, instead layed eggs directly on ledges, especially in the coastal sites (Marín 1997). This might be related to the lack of the proper nesting materials (mosses and liverwoths).

The breeding season of the Black Swift in southern California is spread over 4.5–5 months (Foerster 1987, Marín 1997). Lack (1954, 1968) observed that breeding in most species of birds is timed to occur when food is most abundant, especially in temperate regions.

In the western United States, Chapman (1954) noted that ants swarmed from May through September and that the peak of ant swarming was July. The observed peak of egg hatching in Black Swifts was also July coinciding with the peak of ant swarming (Fig. 5). These data support Holroyd's and Jalkotzy's (*in* Campbell et al. 1990) suggestion that the breeding of the Black Swift in southwestern Canada was timed to the swarming of flying ants (Hymenoptera). In the western U.S. ants swarm in large numbers on mountain and ridge tops for several days (Chapman 1954). The peak time of ant swarming observed by Chapman (1954) was from 07:00 to 14:00 and coincides with the first period of shorter feeding bouts in the Black Swifts (Fig. 3).

Foerster (1987) reported average prey sizes from two boluses (n = 289 prey items) as 9.9 and 10.2 mm, slightly larger than my averages. He did not report sizes smaller than 7 mm or larger than 13 mm. Foster (1987) speculated on possible size selection by the swifts; however, I observed 46.5% percent of prey items below and above those categories (n = 1179 prey items, 10 boluses). The data from this and other studies (Collins and Landy 1968, Foerster 1987) suggest that prey items given to the nestlings are selected not by size but by insect taxon. This is probably a consequence of feeding on insect swarms.

The main diet of Black Swift nestlings at San Jacinto was winged ants, which have a

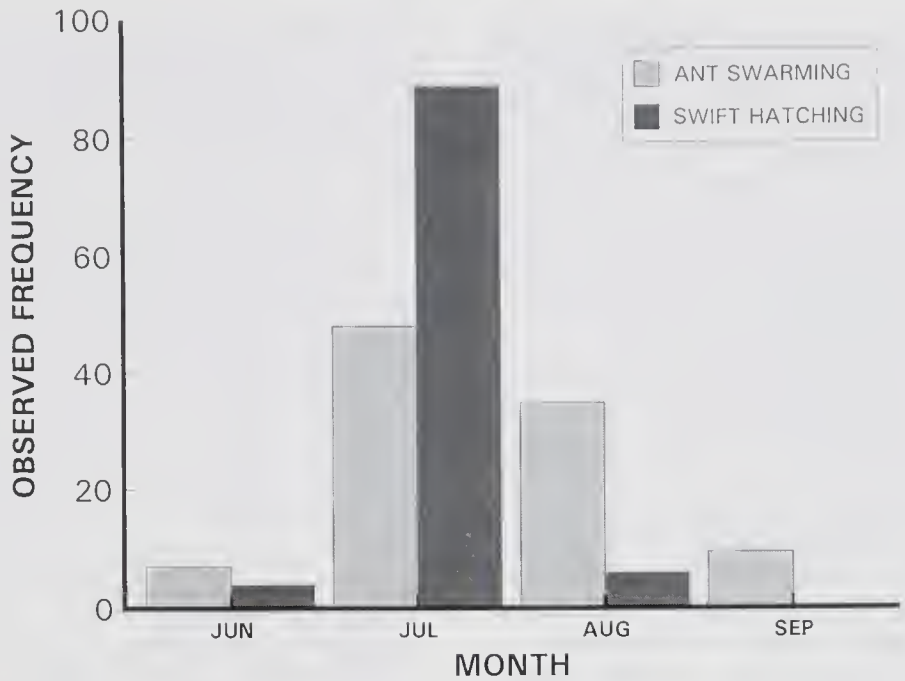

FIG. 5. Frequency of Black Swift hatching and ant swarming in southern California. Data for ant swarming are from Chapman (1954).

high fat content. The large preponderance of winged ants in the nestling diet is similar that of other cypseloidine swifts (Whitacre 1991). The percent fat per dry weight in alate ants ranges from 23.8 to 59.5% in females and from 3.3 to 9.6% in males (Taylor 1975, Redford and Dorea 1984). A nestling of any bird species fed a diet rich in energy could accumulate large amounts of subcutaneous fat. Before fledging the young Black Swift accumulates much visible subcutaneous fat and attains up to 148% of adult body mass; it reaches adult mass at day 15–16 of the nestling period (Marín 1997). The limited inter-year sampling by Foerster (1987) and myself suggests that the swifts at San Jacinto, during the breeding season, may specialize in exploiting local concentrations of 2–3 ant species (*Camponotus* spp.). Winged ants are a temporarily superabundant, patchy, and ephemeral, but lipid-rich food source. Other important prey items included Hemiptera and Homoptera (Table 1).

From scattered observations, (e.g., Michael 1927, Smith 1928, Bent 1940, Collins 1998, Collins and Peterson 1998) there is a general agreement that Black Swift nestlings are fed at long intervals, primarily early in the morning and late in the afternoon or at night. My data corroborate those conclusions (Fig. 3). The alternation of long and short foraging trips resembles the strategy of energy expenditure described for foraging and food delivery in pelagic seabirds. Charurand and Weimerskirch (1994) and Weimerskirch and coworkers (1994) showed that long trips were primarily for parental food storage as well as nestling food gathering, whereas short trips were used to deliver food to the nestlings. Although the duration of seabirds' trips is days, instead of hours as in swifts, they might well serve analogous purposes.

Like seabirds, the Black Swift might gain weight on the long trips and lose it overnight. Black Swifts have a high metabolic rate and lose on average 7.9 % of body mass overnight (Marín, unpubl. data). Thus, the need for the long foraging bout is in accordance with the energy storage hypothesis (Chaurand and Weimerskirch 1994, Weimerskirch et al. 1994). Black Swift migration occurs immediately after the nestlings fledge; other species of swifts (e.g., *Chaetura* spp.) stay a few months after breeding, probably to store some energy for migration (Marín 1997). Accordingly, this long single foraging bout might also serve to store energy for migration, particularly during the later part of the breeding season.

As the Black Swift nestlings increase in age, it seems that the adults feed them only late at night. Quantitative data on feeding

rates or number of trips per day with respect to nestling age are scarce; however, declines in the number of trips per day with nestling age have been reported in other swift species (Malacarne et al. 1992, Oniki et al. 1992).

Lack (1954, 1968) suggested that seabirds with long nestling periods and single egg clutches were energy limited. This energy limitation was in food finding, food delivery, or both. Some swifts, particularly cypseloidines, have life history parameters similar to procellariiform seabirds (Lack and Lack 1951; Lack 1956, 1968; Marín and Stiles 1992; Marín 1993). For example, the Black Swift rears a single, slowly growing nestling, which suggests a constraint in either finding or delivering food. Because Black Swift nestlings require a highly specialized diet in order to have an initial fast growth and acquire a size larger than the adult quickly. I predict that the major constraint is food finding.

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FACTORS THAT INFLUENCE TRANSLOCATION SUCCESS IN THE RED-COCKADED WOODPECKER

KATHLEEN E. FRANZREB[1]

ABSTRACT.—To restore a population that had declined to 4 individuals by late 1985, 54 Red-cockaded Woodpeckers (*Picoides borealis*) were translocated at the Savannah River Site in South Carolina between 1986 and 1995. Translocation success was evaluated by sex, age, and distance between the capture and release site. For moves involving females, the presence of a resident male and the status of the male (breeder, inexperienced, or helper) also was assessed. Of the factors I evaluated, only the distance of the move was statistically significant with increasing success associated with increasing distance. The presence of a resident male at the female's release site led to no more success than releasing the female concurrently with a male; nor did the male's status appear to play a significant role in female translocation success. Overall, 31 of 49 (excluding nestlings) translocated birds remained at or near the release site for at least 30 days, resulting in a success rate of 63.2%. Of the birds that were successfully translocated, 51.0% had reproduced by July 1996. *Received 2 March 1998, accepted 15 Oct. 1998.*

Endemic to the open pine woodlands of the South, Red-cockaded Woodpeckers (*Picoides borealis*) are cooperative breeders whose groups usually consist of a breeding pair and often one or more helpers, usually male offspring (U.S. Fish and Wildlife Service 1985). A series of cavity trees occupied by such a group is referred to as a cluster. These cavities are used year round for night roosting and as nest sites during the breeding season (Steirly 1957). Since 1970 the species has been considered Federally endangered primarily because of widespread habitat loss, which has fragmented the original population into many subunits, some quite small and/or isolated (U.S. Fish and Wildlife Service 1985). One such small population occupies the Savannah River Site in South Carolina.

By late 1985 the number of Red-cockaded Woodpeckers had dwindled to one breeding pair and two single males (DeFazio et al. 1987), and the Forest Service began intensive management to prevent extirpation on the site (Gaines et al. 1995). With the nearest known Red-cockaded Woodpecker population 32 km away, natural recruitment of and colonization by new individuals was considered unlikely. Because Red-cockaded Woodpeckers prefer older, live pine trees for constructing their cavities (Steirly 1957, Jackson et al. 1979, Conner and O'Halloran 1987, Rudolph and Conner 1991) and few trees of sufficient age and diameter were available, Forest Service personnel installed 305 artificial cavities (see Allen 1991 for details on artificial cavity construction and installation). Other management activities have included: (1) restricting cavity access by other larger woodpecker species with metal "restrictor" plates (Carter et al. 1989), (2) removing southern flying squirrels (*Glaucomys volans*) encountered while monitoring cavities and squirrel nest boxes, and (3) improving habitat quality by controlling the hardwood midstory vegetation that causes woodpeckers to abandon their cavities (Conner and Rudolph 1989, Costa and Escano 1989, Hooper et al. 1991, Loeb et al. 1992).

In an effort to stabilize and eventually increase the population at the site, the Forest Service began a program of translocating woodpeckers from populations outside of and within the site. The objectives were to increase the number of breeding pairs, bolster the overall population size, and minimize potential adverse genetic consequences arising from small population size (Allen et al. 1993, Gaines et al. 1995). Here I assess the results of 10 years of Red-cockaded Woodpecker translocations at the Savannah River Site to determine the variables most likely to contribute to successful translocations, an important strategy in the recovery of small, isolated populations.

STUDY AREA AND METHODS

Study area.—The Savannah River Site lies within the Upper Coastal Plain physiographic region in Aiken, Allendale, and Barnwell counties in South Caro-

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lina. By the early 1950s, most of the site was in agricultural use or had been harvested for timber. In 1951, the Department of Energy (DOE) acquired 80,269 ha of contiguous land to develop the area as a nuclear production facility. Under an interagency agreement, the Savannah River Natural Resource Management and Research Institute (U.S. Department of Agriculture, Forest Service) has managed the natural resources on the site for DOE since 1952. Today approximately 69,000 ha on the site are in pine stands (Workman and McLeod 1990), most of which are less than 50 years old although there are some residual older pine trees. The area managed for the woodpecker contains 31,970 ha of pine forest consisting of longleaf (*Pinus palustris;* 37.7% of the pine acreage), loblolly (*P. taeda;* 45.4%), slash (*P. elliotti;* 13.4%), and other (0.2%) pines in addition to pine-hardwoods (3.3%; G. Gaines, unpubl. data).

Field methods.—Beginning in 1980, Red-cockaded Woodpeckers at the Savannah River Site were banded with a U.S. Fish and Wildlife Service aluminum leg band and with a unique color plastic leg band combination for field identification. Birds were banded as nestlings on the site, when first captured as adults, or just prior to release if they were from an offsite population.

Blood samples were taken from adults at the Savannah River Site to determine the relatedness of individuals of unknown heritage and level of genetic heterozygosity (Stangel et al. 1992, Haig et al. 1993). The results helped to provide the genealogical pedigree and verification of parentage needed to determine which individuals should be matched for mating.

Individual translocations either provided a mate for an established breeding bird (e.g., to replace a lost mate) or established a new pair in unoccupied territory. If a translocated bird remained in the vicinity of the release site for at least 30 days, I regarded the release as successful. Preference was given to abandoned clusters that were more than 1 km from other active clusters to minimize interference by other Red-cockaded Woodpeckers.

Translocated individuals and pairs were introduced into groups with an unpaired, resident bird or into abandoned clusters. Trapping, transportation, and release followed the methods described by DeFazio and coworkers (1987) and Allen and coworkers (1993). The age, group, sex, status (such as helper or breeding female), previous breeding experience, distance from the capture to release site, and location of capture site were recorded for each bird translocated. Translocations involved moving an independent subadult (one year or less in age) or adult female to a bachelor male, moving an unpaired female and/or male to unoccupied habitat, moving a family unit (mated pair and nestlings) to unoccupied habitat, and cross-fostering nestlings.

Observations of translocated birds lasted approximately 8–30 hrs per bird the week immediately following release and were repeated at least once per week during the breeding season and once per month during the non-breeding season to monitor each bird's status. If a translocated bird could not be relocated, a thorough search was made in clusters within approximately 0.8 km. For birds captured on the site, the search included previous roost trees even if they were beyond 0.8 km of the release site.

Analytical methods.—How a bird responded to translocation (e.g., stayed at release site, returned home, disappeared), whether or not it eventually reproduced in the vicinity of the release site, and the number of fledglings produced was recorded for each bird. Because the distance between the capture and release site was found to influence the results, the data were examined separately for moves of various distances (≤ 7 km, 19–23 km, 182–483 km).

To evaluate if sex of the translocated bird affected the outcome of a move, translocation success was compared for all males to all females, adult males to adult females, and subadult males to subadult females. To determine if there was a period of time shortly after fledging when younger subadult females were more likely to remain at the release site, the translocation success of subadult females 5–7 months of age was compared to those 7–12 months old.

Distance between the capture and release site was evaluated by examining translocation success for short (≤ 7 km), moderate (19–23 km), and long (182–483 km) distance moves. There are two subpopulations of Red-cockaded Woodpeckers at the Savannah River Site. Moves within either subpopulation were no more than 7 km. The two subpopulations are separated by about 19 km. Hence, translocations onsite between the two subpopulations involved distances of 19–23 km. All offsite populations were at least 182 km from the Savannah River Site. Moves from offsite were done for 7 of 10 years between 1986 and 1995. Capture sites on the Savannah River Site were monitored to determine if released birds returned home. Similar monitoring was not undertaken at offsite populations because they were too far from the Savannah River Site to check routinely.

To determine if the presence of a resident male affected the translocation success of a female, I compared responses of females who were moved to clusters with a resident male (regardless of his reproductive experience) versus a "co-move" in which a male (captured in a separate cluster) was translocated simultaneously with a female to a new site. To evaluate the possible influence of distance from the capture to release site, the translocation success for females moved to resident males and those moved with a male were compared with respect to distance.

The possible effect of male status (breeder, helper, or inexperienced) on female relocation success was examined for females: (1) moved to a resident male, (2) moved simultaneously with a male, and (3) for both situations combined. An "inexperienced" male had no known experience as a breeder or helper. Female translocation success with respect to male status was segregated further by distance moved.

All statistical comparisons were made using Fisher's

Exact Test (Sokal and Rohlf 1995) with the level of significance defined as $P \leq 0.05$ and executed with SAS (version 6.12, Windows 95, IBM-compatible; SAS Institute 1990). Fisher's Exact Test for contingency tables was used because in most cases cell frequencies were too small to support standard χ^2 tests. Unless otherwise noted, the results for the five translocated nestlings are excluded from these comparisons.

RESULTS

From 1986 to 1995, 54 Red-cockaded Woodpeckers were translocated, at first from populations off the site, but later from onsite as their numbers increased. Beginning in 1986, 21 birds were taken from offsite populations: 7 females, 1 male, and 5 nestlings from the Francis Marion National Forest in South Carolina (about 192 km away); 5 females from the Apalachicola National Forest in Florida (483 km away); 1 female from Fort Bragg in North Carolina (266 km away); and 2 females from the Carolina Sandhills National Wildlife Refuge in South Carolina (182 km away). Offsite locations were selected because they contained relatively large numbers of Red-cockaded Woodpeckers. Thirty-three birds were translocated within the site beginning in 1987.

Of the 24 subadult females, 6 remained at the release site and bred, 1 died after remaining more than 30 days, 6 moved to clusters near the release site and bred with nearby males, 1 returned to the capture site, and 10 disappeared. Of the 10, 4 remained at the release site for more than 30 days, 1 was chased away by other Red-cockaded Woodpeckers, and another reappeared five months later approximately 20 km away and became the breeding female in that cluster. Of 9 adult females, 2 remained at the release site and bred, 5 moved to nearby clusters and bred, 1 returned to her original cluster, and 1 remained at the release site but did not breed.

Of 10 subadult males, 2 stayed at the release site and bred, 2 moved to a nearby cluster and bred, 1 remained at the release site for four months then disappeared, 4 disappeared soon after release, and 1 returned home after 30 days. Two adult males remained where released or close by and bred, 1 disappeared in less than two days, and 3 returned home immediately.

Five nestlings were relocated. The first three nestlings were moved with their parents to the Savannah River Site from the Francis Marion National Forest in 1988 and later died from parental neglect (Allen et al. 1993). The other two nestlings were fostered in 1987; both successfully fledged after being placed in a Red-cockaded Woodpecker nest. The female disappeared after five months, and the male became a breeder in a nearby cluster and eventually produced two fledglings.

Ten of the 49 birds (excluding the 5 nestlings) that were moved consisted of pairs of subadult females and subadult males moved concurrently. Overall, 31 of 49 (63.2%) adults and subadults remained at or near the release site for at least 30 days after release and 25 (51.0%) eventually reproduced (Table 1). The number of birds represented in the various combinations of moves segregated by age and cluster status are shown in Table 1.

Translocation was successful for 61.8% of subadults (21 of 34) and 66.7% of adults (10 of 15; Table 2). There were no significant differences in success measured either by the number that stayed or by the number that reproduced for adult males compared to adult females for short, moderate, or long distance moves (Table 2; Fisher's Exact Tests: all $P > 0.05$). Nor was there a difference in success of subadult males compared to subadult females for any of the distance classes (Fisher's Exact Tests: all $P > 0.05$).

Of 189 fledglings produced from 1986–1996, 104 (55.0%) had at least one parent that had been translocated. The number of fledglings excludes the young produced by birds that were translocated but did not remain in the vicinity of the release site to breed (Table 2).

Translocation success of younger subadult females (5–7 months of age) did not differ significantly from those that were older (7–12 months of age; Fisher's Exact Test: $P > 0.05$ for all comparisons). There were no short distance moves involving younger subadult females.

Because sex and age did not appear to influence success (Table 2), I pooled the data and tested for a distance effect. Translocated birds were more likely to stay with increasing distance from their capture site: 25.0% success for translocations less than 7 km, 71.4% for 19–23 km, and 81.3% for 182–483 km moves. The distance a bird was moved had a

TABLE 1. Success of translocated Red-cockaded Woodpeckers by age and type of move at the Savannah River Site (1986–1995).

	Number of birds		
	Translocated	Stayed > 30 days	Reproduced
Translocated to resident male:			
Adult female	5	5	5
Subadult female	17	13	9
Translocated to unoccupied cluster:			
Adult breeding male	1	0	0
Subadult male	5	3	2
Adult female	1	1	1
Adult male/adult female[a]	4	2	2
Adult male/subadult female[b]	4	2	2
Subadult male/subadult female[c]	10	4	4
Adult male/adult female/nestings[d] (family unit)	5	1	0
Fostered nestlings	2	2	1
Total adults and subadults	49	31 (63.2%)	25 (51.0%)
Total including nestlings	54	33 (61.1%)	26 (48.1%)

[a] In one move, the male remained; in the other, only the female remained.
[b] In one move, neither bird remained; in the other, both remained.
[c] In three cases, neither the male nor female remained; in two cases, only the male remained; in three cases, only the female remained; in two cases, both birds remained.
[d] Only the female remained.

highly significant effect on whether the bird remained more than 30 days (Fisher's Exact Test: $P = 0.01$), but was not significant for birds that eventually reproduced (Fisher's Exact Test: $P = 0.12$; Table 3). Birds moved a short distance were more likely to return home [41.7% ($n = 12$) for short versus 4.8% ($n = 21$) for moderate distance moves; Fisher's Exact Test: $P = 0.02$]. There was no significant difference in the success rate of a bird moved a moderate versus a long distance (Fisher's Exact Test: $P > 0.05$ stay, $P > 0.05$ reproduce, $n = 21$ and 16, respectively). Nor was there a significant difference in rate of return for males versus females moved a short (Fisher's Exact Test: $P > 0.05$) or moderate distance (Fisher's Exact Test: $P > 0.05$).

Eighteen of 22 females (81.8%) that were moved to resident males were successful (stayed), whereas 5 of 10 females (50.0%) succeeded that were moved concurrently with a male. Of the 10 co-moves, 3 females remained after the male left and 2 males stayed even though the female departed. In two cases, both male and female remained. In one of the three instances when both members of the co-move left, the female left first and in the other two cases it could not be determined which of the birds was the first to leave. Of the six cases in which the male left, the female remained behind in three of them. Although moving a female to a site where a male already was established was thought to be advantageous, the success rate was not significantly different from situations in which the female was moved simultaneously with a male for either moderate (Fisher's Exact Test: $P > 0.05$ for stay, $P > 0.05$ for reproduce, $n = 14$) or long distance moves (Fisher's Exact Test: $P > 0.05$ for stay, $P > 0.05$ for reproduce, $n = 14$). Nor was there a significant difference in success of females moved either to a resident male or with a male when translocations of moderate and long distances were combined (Fisher's Exact Test: $P > 0.05$ stay, $P > 0.05$ reproduce, $n = 28$). No short distance moves of a female to a resident male were undertaken.

Because female success was not influenced by whether the male already was on the release site or whether he was moved simultaneously with her, these data were pooled. Females had a success rate of 87.5% (seven successes in eight cases) if the male involved was an experienced breeding male, 40.0% ($n = 5$) if he was a helper, and 73.7% ($n = 19$) if the male was inexperienced. Because there were only four short distance moves and none of these involved a breeder male, the effect of male status could not be assessed for females

TABLE 2. Translocation success by sex and age of Red-cockaded Woodpeckers with respect to distance moved at the Savannah River Site (1986–1995).[a]

Sex/age class	Distance moved				No. fledglings produced (No./sex-age class)
	< 7 km	19–23 km	182–483 km	Total	
Adult females:					29 (3.2)
Number translocated	1	3	5	9	
Number stayed (%)	0 (0.0%)	3 (100.0%)	5 (100.0%)	8 (88.9%)	
Number reproduced (%)	0 (0.0%)	3 (100.0%)	4 (80.0%)	7 (77.8%)	
Adult males:					4 (0.7)
Number translocated	4	1	1	6	
Number stayed (%)	2 (50.0%)	0 (0.0%)	0 (0.0%)	2 (33.3%)	
Number reproduced (%)	2 (50.0%)	0 (0.0%)	0 (0.0%)	2 (33.3%)	
Subadult females:					58 (2.4)
Number translocated	3	11	10	24	
Number stayed (%)	1 (33.3%)	7 (63.6%)	8 (80.0%)	16 (66.7%)	
Number reproduced (%)	1 (33.3%)	5 (45.4%)	6 (60.0%)	12 (50.0%)	
Subadult males:					20 (2.0)
Number moved	4	6	0	10	
Number stayed (%)	0 (0.0%)	5 (83.3%)	—[b]	5 (50.0%)	
Number reproduced (%)	0 (0.0%)	4 (66.7%)	—[b]	4 (40.0%)	
All females:					87 (2.6)
Number translocated	4	14	15	33	
Number stayed (%)	1 (25.0%)	10 (71.4%)	13 (86.7%)	24 (72.7%)	
Number reproduced (%)	1 (25.0%)	8 (57.1%)	10 (66.7%)	19 (57.6%)	
All males:					24 (1.5)
Number translocated	8	7	1	16	
Number stayed (%)	2 (25.0%)	5 (71.4%)	0 (0.0%)	7 (43.8%)	
Number reproduced (%)	2 (25.0%)	4 (57.1%)	0 (0.0%)	6 (37.5%)	
Nestlings:					2 (0.4)
Number moved	—[b]	—[b]	5	5	
Number stayed (%)	—[b]	—[b]	2 (40.0%)	2 (40.0%)	
Number reproduced (%)	—[b]	—[b]	1 (20.0%)	1 (20.0%)	
Total includes nestlings				54	104[c]
Total excludes nestlings				49	102[c]

[a] None of the results from Fisher's Exact Tests was significant at $P < 0.05$.

[b] — = not applicable; no tests of this type were made.

[c] Column does not add to 102 or 104 because nine fledglings were produced by parents both of whom had been translocated; total figure includes fledglings produced in 1996.

moved a short distance. For all moves, there was no significant difference in female success when comparing breeder, helper, or inexperienced males (Fisher's Exact Test: all $P > 0.05$).

DISCUSSION

The first reported Red-cockaded Woodpecker translocations involved a 1981 relocation of 12 birds from 5 groups at the Fort Stewart Army Base to St. Catherines Island, both in Georgia (Odum et al. 1982). Five of these birds survived at least eight months and two produced one fledgling in 1981. In 1984 and 1986, two pairs and one single male were moved from private land to the St. Marks National Wildlife Refuge and adjacent Ochlockonee River State Park in Florida in an attempt to enhance the three active groups at the release site (Reinman 1995). One female remained and nested successfully for four consecutive years, one male returned to the capture site, one male died, and the fate of the other birds is unknown. Other translocations have been conducted to establish a group at a site occupied by a single bird (Allen et al. 1993) and to establish new groups (Rudolph et al. 1992, Allen et al. 1993).

Working with data collated from 143 Red-cockaded Woodpecker translocations under a wide range of circumstances, Costa and Kennedy (1994) found various definitions of

TABLE 3. Effect of distance between capture and release site on number of successful translocations of Red-cockaded Woodpeckers at the Savannah River Site (1986–1995).

	Distance moved			
Number of birds	< 7 km	19–23 km	182–483 km	Total
Moved	12	21	16	49[a]
Stayed (%)	3 (25.0%)	15 (71.4%)	13 (81.3%)	31 (63.3%)
Reproduced (%)	3 (25.0%)	12 (57.1%)	10 (62.5%)	25 (51.0%)
Returned home (%)	5 (41.7%)	1 (4.8%)	—[b]	6 (7.5%)

	Fisher's exact test: *P* value		
Distance moved	Stayed	Reproduce	Returned home
All distances	0.01	0.12	
Short vs moderate distance	0.01	0.15	
Moderate vs long distance	0.70	1.00	
Short vs moderate distance			0.02

[a] Excludes nestlings.
[b] — = not available.

translocation success ranging from "interacted well" to "fledged young." They noted successful moves 66% of the time for subadult females (n = 44) and 58% of the time for adult females (n = 33). My study showed an overall female success rate of 67% for subadults and 89% for adults. However, Costa's and Kennedy's results are difficult to compare to mine because they contain a variety of criteria for translocation success. Moreover, in my study there was no significant difference in the success rate based on age (subadult versus adult) for either females or males when considering the distance of the move. Some of my comparisons involve small sample sizes and it is possible that a larger data set may have revealed some significant differences. Additional work is needed to explore more fully any possible differences in success rate based on age of the bird.

My study showed a greater tendency for birds being moved a moderate (19–23 km) or long (182–483 km) distance to remain at the release site and reproduce than birds that were moved short distances (< 7 km). Because there were no moves between 7–19 km, it is not known at what distance the success would equal that of moves more than 19 km. Therefore, at the present time, it is recommended that translocations involve distances of at least 7 km (preferably more) between the capture and release sites to discourage homing by the birds.

DeFazio and coworkers (1987), Hess and Costa (1995), and Reinman (1995) suggest that the most successful translocations of females are those in which the release site contains established single males—a finding supported by earlier translocations of 16 females at the Savannah River Site (Allen et al. 1993). The success rate for translocations to areas that contained single established males was 63.2% for Costa and Kennedy (1994) and 81.0% for my study. However, I found that when the release site contained a resident male, female success was no greater than when a female was moved concurrently with a male for moderate and long distances.

Costa and Kennedy (1994) recommend using a two level standardized definition of success. One level reflects primary evidence of breeding (e.g., copulation, etc.) and the other that the bird has become attached to the site (e.g., roosting in a cluster, etc.). For any translocation effort to succeed, the first major hurdle is for the bird to remain at the release site. In my study, the presence of a translocated bird at the release site after 30 days was considered evidence that the bird had accepted the site and was likely to breed once a suitable mate became available. Because disease and predation may prevent some of these birds from surviving long enough to reproduce, the use of breeding as the criterion of translocation success may be overly conservative. If producing at least one fledgling is used to measure translocation success, then 51.0% of the translocated birds in this study were successful. The success rate was 63.2% if defined

as the number of birds remaining near the release site for at least 30 days.

Translocations at the Savannah River Site have played an instrumental role in restoring the Red-cockaded Woodpecker population from 4 individuals in 1985 to 99 individuals (56 adults and 43 young-of-the-year) and 19 breeding pairs in 1996 (Franzreb 1997). Clearly, the use of translocations as a management tool has been an integral part in the recovery of this nearly extirpated population.

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BANDING RETURNS, ARRIVAL PATTERN, AND SITE-FIDELITY OF WHITE-EYED VIREOS

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ABSTRACT.—We present nine years of return data for individually color-banded White-eyed Vireos and describe patterns of arrival and territory use. Of all opportunities for annual return, 48.3% of males and 50% of females were resighted. Most males arrived between 17 and 30 April, with a median arrival date of 24 April, while most females arrived between 21 April and 1 May with a median arrival date of 26 April; males arrived significantly earlier than females. Older males arrived significantly earlier than younger, as has been reported for several other species. The arrival dates for individual males were consistent across years; an individual's arrival date in one year reliably predicted its arrival date in the next year. Thus, the timing of arrival co-varied with three factors: sex, age, and individual. Nearly all males remained faithful to previous territories, although some shifted so that the new territory overlapped the old. Aspects of our data and those of others suggest our return rates are likely a low estimate of survivorship for the species; the actual survival rate is probably higher.
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Recent studies have strongly indicated that populations of many species of migratory birds in North America are declining. This recognition has invigorated research efforts aimed at documenting various aspects of population dynamics among different species and determining the factors underlying these declines (Terborgh 1980, Lovejoy and Oren 1981, Hagan and Johnston 1992, DeGraaf and Rappole 1995, Rappole 1995, Sauer et al. 1996). These studies are useful in establishing current population status for various species, for monitoring relationships between population status and ecological and demographic factors, and for identifying future research and conservation goals. Several approaches have been employed, including point counts of breeding populations, mist-netting of birds at migration stopovers, breeding bird surveys (BBS), and studies of banded populations of birds on both wintering and breeding grounds (Askins et al. 1990, Payne and Payne 1990, Bibby et al. 1992).

Among the groups of birds in decline are migratory species in the family Vireonidae (Robbins et al. 1989). Two species of vireo are federally endangered in the United States: the Black-capped Vireo (*Vireo atricapillus*) found in Texas and Oklahoma (Grzybowski et al. 1986, USFWS 1991), and a race of Bell's Vireo in California, the Least Bell's Vireo (*V. bellii pusillus*; USFWS 1986, Franzreb 1989). Several other species of vireos have declined in numbers, as determined by the USGS Breeding Bird Survey (BBS; Robbins et al. 1989, Sauer and Droege 1992). A number of studies have addressed different aspects of population dynamics in various vireo species including migration patterns (Remsen et al. 1996, Woodrey and Chandler 1997, Woodrey and Moore 1997), population structure (Grzybowski 1991), aspects of breeding (Graber et al. 1985, Grzybowski et al. 1994, Marvil and Cruz 1989, Barber and Martin 1997), and wintering ecology (Greenberg 1992; Greenberg et al. 1993, 1995). Studies of these types are important for gauging long-term changes in migratory vireo populations and the factors that affect them (Holmes et al. 1989; Lynch 1989, 1992).

One of these Nearctic migrant species is the White-eyed Vireo (*Vireo griseus*), a small passerine that occupies secondary deciduous habitat, thickets, and forest-edge in the eastern United States. Its winter range extends across the southern US from Texas to South Carolina, south through the West Indies, and along the eastern coast of Mexico (Barlow 1980, Hopp et al. 1995). The northern subspecies, *V. g. noveboracensis*, is fully migratory. The southeastern subspecies, *V. g. griseus*, has been reported to migrate (Barlow 1980). However, Bradley (1981) reported that a population near Gainesville, Florida was sedentary,

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with individuals remaining through the winter. The remaining subspecies, *V. g. micrus, V. g. bermudianus, V. g. maynardi,* and *V. g. perquisitor,* are apparently nonmigratory (Barlow 1980, Hopp et al. 1995). Analyses of the data from the BBS suggest that White-eyed Vireos have been declining in parts of their breeding range (Robbins et al. 1989, Sauer and Droege 1992). Efforts to document these declines and determine factors that influence population structure and territory use are important for monitoring long-term changes in vireo populations.

In the present study we report on returns of banded White-eyed Vireos for nine years in southwestern Virginia. Banded White-eyed Vireos have been reported to show site fidelity in their breeding range (Hopp et al. 1995) and on winter territories (Rappole and Warner 1980). We used this fidelity to territories to directly measure return rates of banded individuals. In addition we report on the pattern of arrival in the spring and outline the use of territories by individuals during the breeding season.

METHODS

Most birds were banded on two study sites in Washington and Smyth counties in southwestern Virginia. The two sites, each about 35 ha and located 600–800 m above sea level comprised tracts of secondary deciduous growth, typically favored by this species (Conner et al. 1983, Graber et al. 1985, Hopp et al. 1995). Both areas contained 12–16 contiguous White-eyed Vireo territories. Other birds were banded in the same counties at smaller tracts of 3–12 ha, each with 1–6 territories; 2 of these smaller areas were within 5 km of the main study area in Washington County. For all of these study areas the habitat type was mixed, with approximately 60–80% of the areas constituting suitable habitat for the vireos. We attempted to locate and band birds at all smaller appropriate tracts within about 15 km of the site in Washington County. The principal habitat types in this region are deciduous forest or open pastureland; the presence of habitat appropriate for White-eyed Vireos is limited and typically exists in small areas supporting only a few individuals. All but one male in our study shared at least one territorial boundary with another male; most birds shared boundaries with several other males.

We captured most birds soon after their arrival in late April or early May. Males were easily taken in mist nets as they approached tape playbacks of conspecific song. Our attempts to capture females by intercepting approaches to nests clearly disrupted nesting activities, so we discontinued those attempts. On a few occasions females were captured with males, if they followed them into nets during playbacks. All birds were banded under permit with a unique configuration of USFWS aluminum and plastic color bands.

We began checking for arrivals in known territories and neighboring suitable habitat in the first week of April. Monitoring consisted of listening for singing males in known territories for at least 15 minutes; often we used recorded song to attract males. When detected, males were followed to determine whether they were banded, and to identify the color(s) and configuration for banded individuals. Study areas were checked daily until mid-May; unoccupied territories were then checked at least twice weekly until mid-June. We also checked several other known populations of birds within 15 km of the study areas to potentially detect dispersed birds. We were able to assess returns without recapture by identifying the color-band configurations. Because the males of this species are vocally prolific, it was easy to locate newly arrived males. The arrival dates used in this analysis are restricted to subjects for which we spent at least 15 minutes in the area on the day prior to their first detection, i.e., we were confident they were not present on the previous day. Determining arrival dates for females was more difficult because they are behaviorally cryptic, and because they sometimes changed locations after a day or two. Most reliably, finding males allowed us to locate females. Whenever a male was located, we observed him long enough to determine whether a female was also present. In most cases, changes in the males' behavior was indicative of pairing status; unpaired males usually sang at high rates from high, exposed perches, while paired males typically spent more time in lower areas and sang at lower rates (Hopp et al. 1995). Because newly paired males stay close to females it was relatively easy to assess pairing status. Because females were mostly unbanded, determining whether a particular female was a new arrival or had moved from a neighboring male's territory was not possible. Arrival dates for females could be unambiguously determined by assessing the total number of females on the entire study site, with changes between successive days indicating new arrivals. Arrival dates for females used in this analysis are only those we could definitively determine to be new arrivals.

We considered an individual's territory to be the total area the bird was observed to occupy throughout the course of a season without outside influence either by other birds or by the researchers. Site fidelity was then defined as use of an area that overlapped a territory from the previous year by at least 50%. Approximately two-thirds of the males also served as focal subjects for studies of vocal communication, and hence provided more complete data on territory use.

We also examined the encounter records for White-eyed Vireos from the Bird Banding Laboratory (BBL) through 1996. These records include encounters within the same 10′ block (prior to 1958) and document individuals encountered outside the original 10′ block where they were banded. These records potentially provide information about the dispersal of both hatch-

TABLE 1. Returns of male White-eyed Vireos known to be at least one year old when banded.

Banding year	Number banded	Returns in years following banding					
		One	Two	Three	Four	Five	Six
1985	8	3	2	2	1	0	—
1986	4	3	2	1	1	1	0
1987	11	7	4	1	1	1	0
1988	11	5	3	0	—	—	—
1989	14	10	1	1	0	—	—
1990	13	8	6	0	—	—	—
1991	13	4	1	0	—	—	—
Total	74	40	19	5	3	2	0
Percent[a]		54	26	7	4	3	0

[a] Calculations based on percent returns relative to banding year.

ing year (HY) and adult (after hatching year; AHY) birds. To assure that we were assessing dispersal rather than migratory movements, we considered only birds with both banding and encounter dates between 16 May and 16 September inclusive. These dates are well within the average spring arrival and fall departure dates for this species throughout most of its range (see appendix 1 in Hopp et al. 1995).

RESULTS

Returns of banded birds.—During the breeding seasons of 1985–1991, we banded 74 adult male birds used in this analysis. We also banded 5 females and 42 nestlings/fledglings, most of which were known to have survived until they were capable of sustained flight. Returns of males for each year from 1986–1994 individually and combined are given in Table 1. The percentage returns are based on combined data from nine years, computing the number that return relative to the banding year. Because these subjects were all banded as adults (AHY), these percentages give an indication of survivorship in the successive years following banding. The two individuals surviving five seasons after banding were thus at least six years old. Our oldest bird (not included in this analysis) arrived as an AHY bird in 1990 and was still alive in the summer of 1998, making him at least 9 years old.

Calculating the probability of return given that a bird was alive in the previous year, 40 of 74 (54.1%) returned the year following banding, 19 of 40 (47.5%) returned the second year, 5 of 19 (26.3%) returned the third year, 3 of 5 (60.0%) returned the fourth, 2 of 3 (66.7%) returned the fifth year, and none of 2 returned the sixth year following banding. Over the nine year period, there were 143 opportunities for return and 69 documented returns. Thus the percentage of male White-eyed Vireos returning in any year, given the bird was known to be alive the previous year, was 48.3%. Of the five females banded, three returned in the year following banding and one individual returned in the second and third years following banding. Of the ten opportunities for female returns, five (50.0%) were resighted. We did not recover any of the birds banded as nestlings or fledglings.

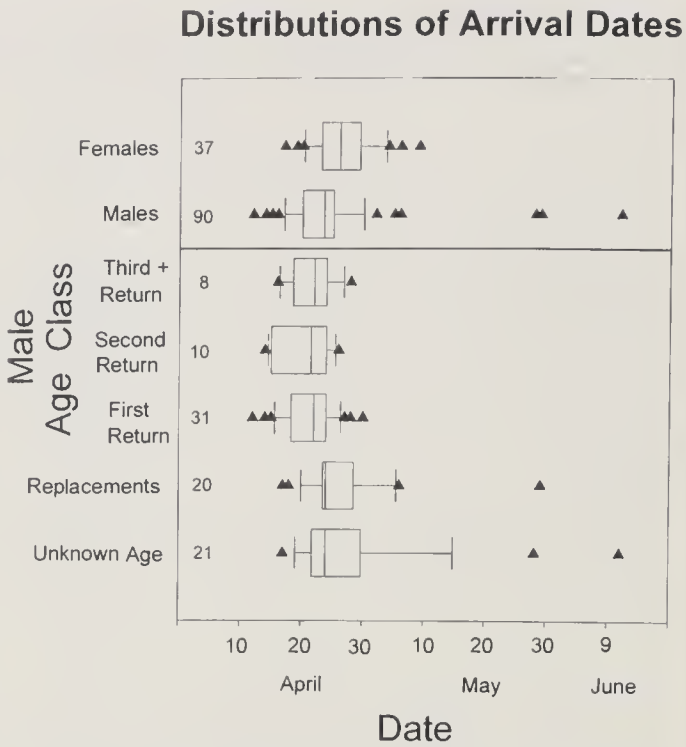

FIG. 1. Box plot of arrival dates for all females and males. Males are further divided into various age classes (see text for explanations). For each plot the total box encompasses the second and third quartiles for each distribution, with the central vertical line showing the median arrival date. Horizontal lines show the 10–90% range of dates, and triangles indicate individual arrival dates in the outlying 10% ranges.

Male arrival pattern.—We obtained 90 arrival dates from 63 individuals. The combined dates ranged from 12 April to 11 June with a median arrival date of 23 April (Fig. 1). Most birds arrived during the two weeks between 16 April and 30 April (75 of 90: 83.3 %). There were six arrival dates prior to 16 April, with three of these from the same banded individual in successive years. Eight arrival dates were after 30 April, five of these in early May (2 May, and two each on 5 May and 6 May) and three were well outside the distri-

bution of other arrivals—28, 29 May and 11 June. These three extremely late unbanded individuals likely represent relocations rather than arrival dates (see below).

Female arrival pattern.—We obtained 37 arrival dates for females. Of these only 4 were from returning, banded individuals, the remainder from unbanded individuals. The combined dates ranged from 17 April to 9 May, with a median arrival date of 26 April (Fig. 1). Most of the arrival dates fell in the ten day period between 21 April and 1 May (28 of 37: 75.7%). Two of the four earliest arrival dates (17 and 20 April) were from returning banded individuals. Because females are cryptic in their plumage and behavior and because we assessed their arrival primarily by pairing with males, our sampling was likely biased toward the earlier arrival dates. Despite this, the median arrival date for females was later than all of the individual male arrival date categories (Mann-Whitney Test: $U = 3.43$, $P < 0.001$; see Fig. 1). We typically observed several males on territory before any females arrived. In several years, most male territories were occupied before any females were seen.

Age-related male returns.—We recorded 49 arrival dates from returning banded males and 41 from unbanded males that were later banded. Of the unbanded birds, 21 were of unknown age. The remaining 20 arrival dates were from unbanded birds that occupied territories previously occupied by non-returning banded individuals. Given the high site fidelity for returning individuals, this second category of unbanded replacement birds possibly were second-year adults (SY; first breeding season) which were treated separately in our analysis of age-related returns.

Figure 1 shows the distributions of arrival dates for various age-related classes of males. Because the sample sizes in the three oldest age categories were too small to permit statistical comparison across all age categories, we combined all dates of birds returning after three years into one category (four years or older, $n = 8$). To avoid pseudoreplication, in analysis we averaged dates for individuals that contributed more than one arrival date to this combined category, yielding an effective sample size of 5. A comparison of the four male groups, previously unbanded birds, first returns, second returns, and third + returns, was significant (Kruskal-Wallis Test: $H = 11.27$, $P < 0.05$). In post hoc (Bonferroni) pairwise comparisons, the only significant difference was between the new (unbanded) arrivals and the first return year ($Z = 2.77$, $P < 0.05$), indicating that the gain in arrival is between the first (banding) year and the first return year. In a more conservative version of this comparison, we compared all returning, banded birds to all unbanded birds. This comparison was also significant, showing arrival dates of all banded birds to be earlier than arrival dates of all unbanded birds (Mann-Whitney Test: $U = 3.66$, $P < 0.001$). In a more direct test, we compared successive dates from individuals for whom we obtained arrival dates in two consecutive years ($n = 32$ pairs). This comparison was only marginally significant when using all consecutive arrival pairs (Wilcoxon Test: $Z = 1.465$, $P = 0.074$). When this analysis was restricted to consecutive-year pairs starting with the first (unbanded) year, the comparison was significant (Wilcoxon Test: $Z = 1.80$, $P < 0.05$, $n = 14$), showing that birds arrived earlier in the second of these two consecutive years, and reinforcing the finding that the gain in arrival dates is apparent only between the banding and subsequent year. For the 32 pairs of consecutive year arrival dates, we also found that the arrival date of individuals was a significant predictor of its arrival date in the subsequent year ($r = +0.616$, $P < 0.001$). Thus, while a portion of the variability seen in arrival dates can be attributed to age, a substantial portion can be attributed to individual-specific differences in arrival, with early and late arrivers remaining early and late arrivers respectively across seasons (Fig. 2).

Site fidelity.—Of the returning banded males, 67 of 69, or 97% of returns were to their previous territory. The two individuals observed to move to non-overlapping territories between years both remained within 800 m of their original territory. Several birds enlarged their territories in subsequent years, occupying areas that included their previous territory. Seven individuals disappeared during the course of a season; three returning birds and four birds in the year they were banded. None of these seven birds was seen in subsequent years. One of the three returning birds lost his territory to human habitat clearing

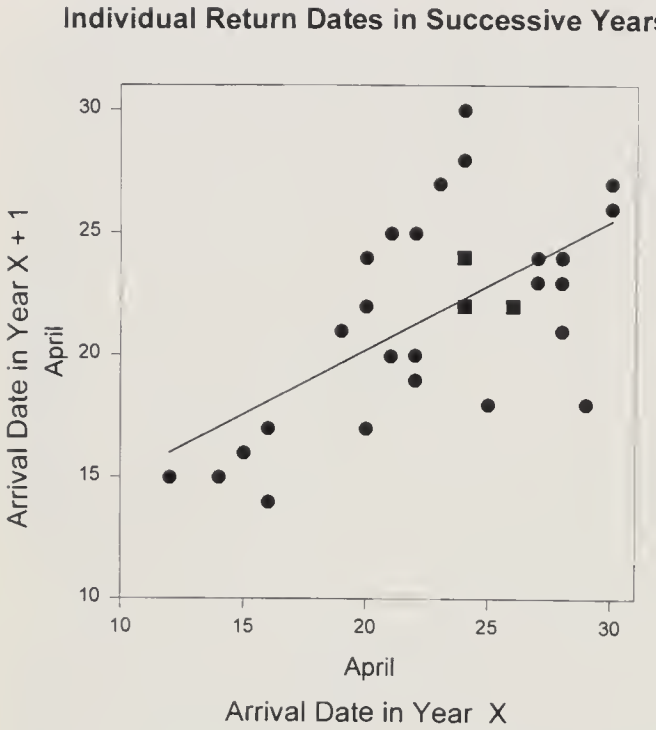

FIG. 2. Scatter plot showing return dates obtained from individual males in successive years. Line depicts best-fitting regression line; squares denote 2 overlapping data points.

during the winter. He was seen in adjacent and nearby territories for only five days following his arrival. Two of the four birds that disappeared during the year they were banded reappeared later in the season. One of these arrived on 22 April in a territory previously occupied by a non-returning banded individual. He was banded on 24 April, disappeared on 2 May, then reappeared on the same territory 7 June where he remained for the season.

For females, all returns were to the same study area where they were first banded, but none to the same territory; none paired with the same male in more than one year. The nearest movement was to an adjacent territory. The farthest moved three territories away, i.e., two intervening territories from the previous year, a distance of about 750 meters.

Territory use.—Territory use in this species is a typical "type A" territory (Nice 1941), with males aggressively defending territories against other males, and with the area used for mating, nesting, and feeding for both adults and young during the breeding season. The defense of territory is usually by a series of behavioral displays, including singing, and less frequently by direct contact (see description by Bradley 1980). Most territorial encounters occurred early in the season, prior to the arrival and pairing with females; following the onset of nesting activities these territorial encounters were rare.

Individual males could easily be tracked during the season, and adults remained on territory into September; the latest date we recorded a bird on territory in autumn was 6 October. During the last few weeks in the fall the adults increased their singing rate and again became quite responsive to tape-recorded song.

Female use of territory was less easy to observe. On several occasions we observed two females within the same territory, always early in a season. In no case did we observe interactions between females indicating territory defense. On one occasion we observed two females within a few centimeters of each other with no overt behavioral response.

As with females, HY birds were difficult to track carefully during a season. Typically, banded young could be found in their natal territories for 4–5 weeks; often birds from the same brood were found together. After this time, banded HY birds began to disperse from their natal territories mid-August through early September, often being found in other territories within the study site. A few HY birds would defend small territories, responding aggressively to tape-recordings with approach and/or singing. Most HY birds left the region on migration prior to the onset of banded AHY bird departures.

USFWS encounter data.—There were 81 total White-eyed Vireo encounter records from the Bird Banding Laboratory. Of these, 22 were both banded and encountered within the 16 May to 16 September period, all of these encountered during the breeding season in the first year after banding. Of these 22, 18 were AHY birds, three were HY, and one was local status (incapable of sustained flight; presumably nestling). Of the 18 adults, 14 were encountered in the same 10′ block in which they were banded. Of the four adults encountered outside their initial banding 10′ block, three were encountered in the next 10′ block of latitude (approximately 19 km on average) and one was encountered in the adjacent 10′ block of longitude (approximately 15 km). Of the three HY birds, one was encountered in the original block, and the other two were en-

countered one 10′ block of latitude and one 10′ block of longitude respectively from where originally banded. The local-status bird was encountered in the same 10′ block where it was initially banded. Two other records deserve mention. One HY bird was banded on 17 August and encountered approximately 155 km away in the following year on 14 May. The other, a local bird, was banded on 12 June and encountered the following 13 May, approximately 190 km from initial banding location. As both of these birds were banded and encountered in states near the northern edge of the species' range (Massachusetts and Maryland respectively), these encounters in the middle part of May likely represent an encounter on their breeding ground rather than a point in their migration paths.

DISCUSSION

Returns of banded birds.—Our overall percentage returns of 48.3% for males and 50% for females gives an indication of the baseline returns expected for this species. These can be compared to return rates reported for Black-capped and Bell's vireos. In a long-term study of Black-capped Vireos, Grzybowski (1991) reported male returns of 65% for a study population of approximately 250 birds. Perhaps more directly comparable were his return rates for approximately 130 males from scattered study locations. For these he reported a return rate of 58%, slightly higher than in our study. For females, he reported 52% and 41% encountered for larger and more scattered study groups, respectively. Similarly, for Bell's Vireos, Greaves and Labinger (1998) reported male returns of 62.5% and 58.6% for two separate study areas, and 57.1% and 58.8% for females from the same two study groups. Two notable differences between the studies of both these species and our study are the sample sizes and the study areas. Grzybowski (1991) reported his percentage returns on samples of approximately 250 and 130 males in the main and scattered study areas. The study by Greaves and Labinger (1998) reported on returns from a smaller number of males: approximately 40 and 30. The study areas, however, were considerably larger than in our study. Many researchers have noted that the percentages of birds re-encountered in banding studies is directly related to the size of the study population, with larger populations affording a higher re-encounter percentage, and that site fidelity is greater in larger study groups (e.g., Temple and Cary 1988, Payne and Payne 1990, Grzybowski 1995). Applied to this study, then, our reported return rates likely represent a low return estimate for the species. The data presented here provide a baseline rate of returns for adult White-eyed Vireos. Because the population densities in this region are relatively low (Price et al. 1995), comparative studies in other areas of this species' range are needed to determine which aspects of the data observed here are shared in other regions, and what factors might affect return rates and survival of White-eyed Vireos.

Arrival patterns.—Our finding that older birds arrive sooner than younger birds in spring is consistent with similar reports in other species (e.g., Nolan 1978, Bedard and LaPointe 1984, Hill 1989, Morton and Derrickson 1990). An earlier arrival could provide either a longer potential breeding season or better chances of obtaining a mate (see Møller 1990). However, the variation we saw was modest; the only significant difference was approximately 2 days gained between the first (banding) year and the first return year, a pattern seen with both the between-subject and within-subject comparisons. It's difficult to argue strongly for a significant pairing advantage, particularly because most males arrive before most females. We have found that the arrival date itself is not a significant predictor of either pairing date or probability of obtaining a mate. Rather, the age of the individual is more likely a factor, i.e., females are more likely to pair with older (returning) males, regardless of arrival date (SLH, unpubl. data). However, the relation between arrival date and reproductive success in White-eyed Vireos is unknown.

Several studies have identified reasons for earlier arrival dates by older birds, and several of these might pertain to White-eyed Vireos (see Ketterson and Nolan 1983, Woodrey and Chandler 1997 for summaries). First, older birds might winter further north than younger birds. However, the site fidelity of White-eyed Vireos to winter territories (Rappole and Warner 1980) argues against this. Second, older birds might leave earlier for northern mi-

gration in the spring. Third, older birds might be better at finding their territory once they have arrived on the breeding grounds. Finally, it is possible that older birds travel faster during spring migration, either through superior navigational skills or more efficient foraging while enroute.

Our finding that the arrival date for an individual in a given year predicted its arrival in the subsequent year is a pattern that to our knowledge has not been previously reported for any species. The variation seen as a result of individual differences accounts for more of the arrival date variability than that seen for age related return dates. The factors outlined above for age related returns may also be used to explain this result, but with individual rather than age related differences in these abilities being applied to individuals initiating spring migration from a common wintering location. Alternatively, this pattern could result from individuals commencing from a wide range of geographic origins, with more northerly-wintering individuals arriving earlier. The relationship between the winter and breeding locations of individuals is unknown.

Philopatry and territory use.—Male White-eyed Vireos show a high degree of territory fidelity. Some researchers have distinguished between site fidelity, where birds return to the study area but to a different territory, and territory fidelity, where birds return to their previous territory (Greenwood 1980, Greenwood and Harvey 1982, Holmes and Sherry 1992). The extent to which birds move between territories in consecutive years has been called breeding dispersal by Greenwood (1980). In our study, the attachment to particular territories is remarkably high and the two tendencies, site and territory fidelity, appear essentially the same. While perhaps uncommon, three lines of evidence may indicate that breeding dispersal movements occur in White-eyed Vireos. First, on two occasions we observed individuals disappear only to reappear in the same territory later within the same season. While we did not locate these birds on other study areas, they obviously relocated for at least a portion of that season. Grzybowski (1995) reported that male Black-capped Vireos sometimes sequentially occupied two noncontiguous territories, and this might also occur in White-eyed Vireos. Second, records from the BBL show four relocations of adult White-eyed Vireos between breeding seasons, with distances of between 15 and 20 km for each. While these records are limited, they nevertheless show that adult White-eyed Vireos are known to relocate between breeding seasons. Third, we observed three arrival dates of individual males in late May and early June, well outside of the migration dates known for this species (Hopp et al. 1995, Remsen et al. 1996). While circumstantial, these late dates likely reflect instances of relocating individuals rather than first-time arrivals. Taken together, these lines of evidence suggest that at least some portion of adult birds tend to disperse from one breeding territory to another, both within and between seasons. This also suggests that our return percentages represent a low estimate of survival for the species.

We observed that HY birds depart from the breeding grounds before AHY birds. This earlier departure of young may be related to an unusual pattern of molt described for White-eyed Vireos, where juveniles exhibit a partial replacement of primaries prior to fall migration, perhaps facilitating migration in HY birds (Lloyd-Evans 1983). This pattern of molt, however, may vary geographically (George 1973). Whether departures of HY birds precede adults in other parts of their range is unknown. The timing of fall migration between HY and AHY White-eyed Vireos is not significantly different in the southern United States. Woodrey and Moore (1997) found that AHY and HY White-eyed Vireos did not differ in their distribution of arrivals. This timing pattern is in contrast to Red-eyed Vireos (*V. olivaceus*) whose adults depart significantly earlier than the young, and the two age-classes apparently migrate at different rates (Woodrey and Chandler 1997). Perhaps while young White-eyed Vireos depart earlier, the adults minimize the timing differences by the time the two groups reach the southern United States. Alternatively, our observed earlier departure of HY birds may signal the onset of a pre-migration dispersal by young birds, followed by their actual southerly migration some time later.

Our failure to recover any SY birds banded as young may stem from several factors. First, it is possible that young birds tend not to re-

turn to the natal area. For many species, a dispersal of young provides an effective mechanism for avoiding inbreeding (Greenwood and Harvey 1982, Davis and Howe 1992), although some young of other vireo species return to their natal area (see below). Alternatively, since White-eyed Vireos inhabit a successional window of habitat it may be in the best interest of young birds to disperse to other areas, because the optimum successional window will eventually close in their natal area. Young birds may disperse from their natal areas to locate suitable breeding habitat for the following spring (e.g., Brewer and Harrison 1975). Second, it is possible that the combination of a modest number of birds banded and relatively small study areas simply precluded our re-encounter with young. In the BBL encounter records there were six reported recoveries of banded HY birds in later years; two were encountered in the original 10′ block, two were encountered 15–20 km of initial banding location, and two were encountered 150–200 km away from the original banding block. These records are equivocal in suggesting a modal pattern of natal dispersal for the species. Instead the pattern appears complex, with distance depending perhaps on other factors, such as habitat size and composition, bird densities, or hatching time of year. In Black-capped Vireos, young birds show a gradient of natal dispersal to at least 21 km (Grzybowski 1991). For this species, the return percentages were directly related to size of the study area, with fewer returns in smaller areas (Grzybowski 1995). In Bell's Vireos, natal dispersal is complex, with some young returning to their natal area, and others dispersing up to 300 km (Kus 1995, Greaves and Labinger 1998). Greaves and Labinger (1998) found that early and late (before and after 15 June, respectively) cohorts of HY Bell's Vireos exhibit significantly different degrees of natal philopatry, with earlier young returning at higher rates. For both Black-capped and Bell's vireos, reported return percentages of young from various studies were 15–27% (Greaves 1987; Grzybowski 1991, 1995; Greaves and Labinger 1998). Our lack of returns provides us with little information on natal dispersal and survival, and instead raises questions about dispersal dynamics of this species.

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RESPONSE OF BROWN-HEADED NUTHATCHES TO THINNING OF PINE PLANTATIONS

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ABSTRACT.—Brown-headed Nuthatches (*Sitta pusilla*) reached their highest abundance within loblolly pine (*Pinus taeda*) plantations in the first year after thinning and declined in subsequent years. Commercial thinning of plantations resulted in a reduction of canopy cover, hardwood basal area, and understory density. Overall, the detection rates of nuthatches were low (19% of points surveyed) and no nuthatches were detected in stands before thinning. Nuthatches were more than three times as likely to be detected within survey points containing snags compared to those that did not. However, snag density did not vary significantly between stand ages. These patterns suggest that nuthatch distribution within stands may be influenced by snag distribution but that distribution among stands may be determined by the density and height of understory vegetation. *Received 13 March 1998, accepted 15 Sept. 1998.*

Prior to European settlement of North America, the Southeastern Coastal Plain was characterized by old-growth pine forests that covered more than 24 million ha (Croker 1979). This ecosystem was maintained by low-intensity ground fires caused by lightning strikes (Komarek 1964, 1974) and indigenous people (Bartram 1791, Ware et al. 1993). Fires occurred over vast areas at approximately 3–5 year intervals (Chapman 1932, Krusac et al. 1995) and maintained forests with an open midstory and dense ground cover of forbs and grasses (Platt et al. 1991).

Land clearing for agriculture, harvesting of longleaf pine (*Pinus palustris*) for the naval stores industry, and the suppression of wildfires severly reduced the extent of the southeastern pine ecosystem by the early 1800s (Ashe 1894, 1915; Pinchot and Ashe 1897). Currently, natural stands of longleaf pine are restricted to only about 1% of their former range (Ware et al. 1993).

Brown-headed Nuthatches (*Sitta pusilla*) are among a small group of species including the Red-cockaded Woodpecker (*Picoides borealis*) and the Bachman's Sparrow (*Aimophila aestivalis*) that are endemic to the southeastern pine ecosystem (Jackson 1988). The Red-cockaded Woodpecker and the Bachman's Sparrow have experienced significant population declines within the southeast region (Lennartz and Henry 1985, Dunning 1993); however, both have benefited from management practices that produce a habitat structure similar to the historic southeastern pine ecosystem (Gobris 1992, Plentovich et al. 1998).

The Brown-headed Nuthatch has also experienced a contraction of its former range (Jackson 1988), and according to data from the U.S. Fish and Wildlife Service's Breeding Bird Survey has been declining at a rate of more than 1.5% per year throughout much of the Southeast (Sauer et al. 1997). Very little is known about the ecology and habitat requirements of the Brown-headed Nuthatch and even less is known about how current forest management practices may affect its distribution. The purpose of this paper is to present some information on the use of pine plantations by Brown-headed Nuthatches relative to stand age and commercial thinning.

METHODS

This study was conducted in managed loblolly pine (*Pinus taeda*) plantations in eastern North Carolina (approximately 35° 50′ N, 77° 00′ W). These plantations are managed for pulpwood and sawtimber production on a 30–35 year rotation. After canopy closure, the plantations are thinned twice before final harvest. Thinnings reduce the number of trees, open the forest canopy, and allow for growth of understory vegetation.

We selected stands that represented seven different ages and relation to thinning: (1) 9–11 year old stands with closed canopies, (2) 13–16 year old stands within one year after the first commercial thinning, (3) 16–18 year old stands that were three years after first thinning, (4) 19–21 year old stands that were 5 years after first thinning, (5) 22–26 year old stands that were within 1 year after second thinning, (6) 28–29 year old stands that were 3 years after second thinning, and (7) 30–35 year old stands that were 5 years after second

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thinning. Six replicate stands (each > 24 ha) were selected for each stand type. Within each stand age, stands were chosen to minimize variation in planted stocking level and basal area of pine. Stands within each type were separated by at least 500 m.

Seven minute, fixed-radius (50 m) point counts were used to measure the density and frequency of occurrence of Brown-headed Nuthatches within study plantations. Four point counts were established within each stand and distributed evenly between edge and interior locations. Edge points were positioned 50 m from the stand edge such that the plot perimeter was tangential to the stand edge. For all stands, edge points were positioned on stand edges that were adjacent to logging roads. Interior points were positioned 150 m from the stand edge. Stands were surveyed three times between 1 June and 4 July 1997. Surveys were initiated 0.5 hr after sunrise and concluded within four hours.

The vegetation was sampled within all point count plots to determine (1) vegetation changes across the growing period, (2) vegetation responses to thinning, and (3) relationships between nuthatch distribution and vegetation. Linear transects were used for vegetation sampling parallel to the long, regularly distributed canopy openings created by row thinning. The length of vegetation transects was standardized to 25 m and the width varied between 4 and 7 m to accommodate variation in thinned and non-thinned longitudinal rows within stands. Four vegetation transects were established within each point count and equally distributed between thinned and non-thinned rows.

Habitat data were collected at two levels within transects. Counts of all large woody plants (> 8 cm dbh) and dead standing stems (snags) by type (hardwood vs pine) and stem diameter class (8–23, 24–38, > 38 cm dbh) were made over the entire 25 m transect. Pine and hardwood basal areas were estimated using the midpoint dbh for the two smaller diameter classes and 38 cm for the larger class (few trees were larger than 38 cm dbh). Additional information was collected within 2 × 2 m quadrats established at opposite ends of each transect. Information collected included canopy cover (measured in four cardinal directions of a compass by convex densiometer) and canopy height (measured using a clinometer), groundcover height and counts of all stems, shrubs, and saplings (> 0.5 m in height and < 8 cm dbh). Counts were summed to represent total groundcover density (stems/m^2).

A Kruskal-Wallis test was used to test for the influence of stand age on all habitat variables except for counts of snags. Because of the many zero values for counts of both Brown-headed Nuthatches and snags (i.e., data were distributed as a negative binomial), frequency of occurrence values were used to assess patterns among stand types. The relationship between nuthatches and habitat variables was assessed at the level of the point count using Kendall's rank correlation. Nuthatches were not detected in 9–10 year old stands, so this stand age was eliminated from all analyses and used only for descriptive purposes.

RESULTS

Stand age had a significant influence (Kruskal-Wallis test: df = 5, $P \leq 0.01$) on all habitat variables measured except the density of snags (Table 1). Canopy height and ground cover height were positively related to stand age whereas pine density was negatively related to stand age. All other significant variables increased with stand age but were also influenced by commercial thinning.

Detection rates for Brown-headed Nuthatches within pine plantations were relatively low. Nuthatches were detected in 15 of 42 (35.7%) pine stands included in the study and 32 of 168 (19%) individual point counts surveyed. Stand age had a significant influence on the detection of Brown-headed Nuthatches ($\chi^2_{\text{Yates Correction}} = 12.3$, df = 5, $P < 0.05$; Fig. 1). No nuthatches were detected in forest patches prior to first thinning. The number of points where nuthatches were detected was greatest in the year immediately following thinning and declined with time after thinning. Using survey points as statistical units, nuthatches were significantly associated with habitat variables that were directly influenced by thinning events. For example, nuthatch abundance was negatively correlated with canopy cover (Kendall $\tau = -0.12$, $n = 144$, $P < 0.03$), hardwood density ($\tau = -0.14$, $n = 144$, $P < 0.02$), and basal area of hardwoods ($\tau = -0.13$, $n = 144$, $P < 0.02$). In addition, nuthatch abundance was positively correlated with groundcover density ($\tau = 0.19$, $n = 144$, $P < 0.001$). Nuthatch density was not significantly correlated with canopy height ($\tau = -0.04$, $n = 144$, $P > 0.05$), pine density ($\tau = 0.04$, $n = 144$, $P > 0.05$) or pine basal area ($\tau = -0.02$, $n = 144$, $P > 0.05$).

Although stand type did not have a significant influence on the number of survey plots containing standing snags, and snags did not appear to result from thinning, nuthatches were positively correlated with standing snags ($\tau = 0.15$, $n = 144$, $P < 0.009$). In fact, nuthatches were over three times more likely to be detected within survey plots containing standing snags (12 of 32 plots, 37.5%) compared to plots that did not (13 of 122 plots, 11.6%; $\chi^2 = 7.35$, df = 1, $P < 0.007$).

DISCUSSION

It is generally thought that partially rotted wood is a prerequisite for cavity excavation

TABLE 1. Habitat characteristics of 7 stand types selected for study ($n = 6$ each). Median values are presented for all habitat variables except for snags where frequency of occurrence is presented.

Habitat variable	Stand age						Test statistic[a]	P
	9–10 years	1 year after first thin	3 years after first thin	5 years after first thin	1 year after second thin	3 years after second thin	5 years after second thin	
Canopy height (m)	17.5	18.1	19.4	21.9	23.2	25.3	26.3	113.4	< 0.01
Canopy cover (%)	96.6	77.1	84.9	86.4	82.7	94.9	95.2	78.1	< 0.01
Pine density (stems/ha)	1070.0	287.1	330.0	210.0	160.0	190.0	170.0	65.4	< 0.01
Pine basal area (m^2/ha)	35.3	8.0	11.0	11.8	12.2	20.9	20.4	78.9	< 0.001
Hardwood density (stems/ha)	0.0	17.4	100.0	90.0	70.0	120.0	150.0	20.7	< 0.001
Hardwood basal area (m^2/ha)	0.0	0.0	7.0	6.3	4.6	7.9	10.5	22.9	< 0.01
Snag frequency (# of points detected)	5	7	6	3	8	5	3	3.35	> 0.05
Groundcover density (stems/m^2)	4.8	8.4	7.1	7.5	10.1	6.9	9.5	15.3	< 0.01
Groundcover height (m)	1.0	1.5	1.5	2.0	2.0	2.3	2.5	112.1	< 0.01

[a] Test statistic and associated P values are based on Kruskal-Wallis ANOVA (H, df = 5) results except for snag frequency which is based on results from a χ^2 test (df = 5) with Yates correction factor.

by Brown-headed Nuthatches, and the majority of cavities reported have been located in snags (McNair 1984). In general the population density of cavity-nesting birds is positively related to snag density (Cunningham et al. 1980, O'Meara 1984, Raphael and White 1984). In Florida, a large percentage of the variation in the density of cavity-nesting birds (including Brown-headed Nuthatches) was explained by snag density and dispersion (Land et al. 1989). Snag density has been shown to be lower in pine plantations than in natural stands (McComb et al. 1986), and was low in the plantations we surveyed. Brown-headed Nuthatches were significantly more likely to be detected within survey points that contained snags. The possibility that snag density may serve to limit overall nuthatch density within loblolly pine plantations requires further investigation. Because nuthatch density was influenced by thinning and snag density, snag density alone does not explain nuthatch distribution among pine stands.

Brown-headed Nuthatches exhibited a rapid response to thinning. Nuthatches were not detected within pine plantations prior to the first thinning but reached their highest densities within the first year after thinning. This response suggests that thinning activities may, in some way, enhance habitat structure for nuthatches. Thinning activities were shown to reduce canopy cover, reduce the density and basal area of hardwoods, and increase groundcover density.

Although the importance of canopy cover to the use of pinelands by Brown-headed Nuthatches has not been explored, Engstrom and coworkers (1984) reported that nuthatch abundance declined as the density of midstory hardwoods increased. This result is consistent with our observations that nuthatches were less common in years after thinning, as the density and basal area of hardwoods increased.

The effects of burning hardwoods on stand use by Brown-headed Nuthatches is similar to that of thinning. Nuthatches used (45 nuthatches/km^2) mature longleaf pine stands that were regularly burned in Florida (Repenning and Labisky 1985), but not stands with well developed understories (Hirth et al. 1991). Nuthatch density decreased with time following burning (Engstrom et al. 1984, Wilson et

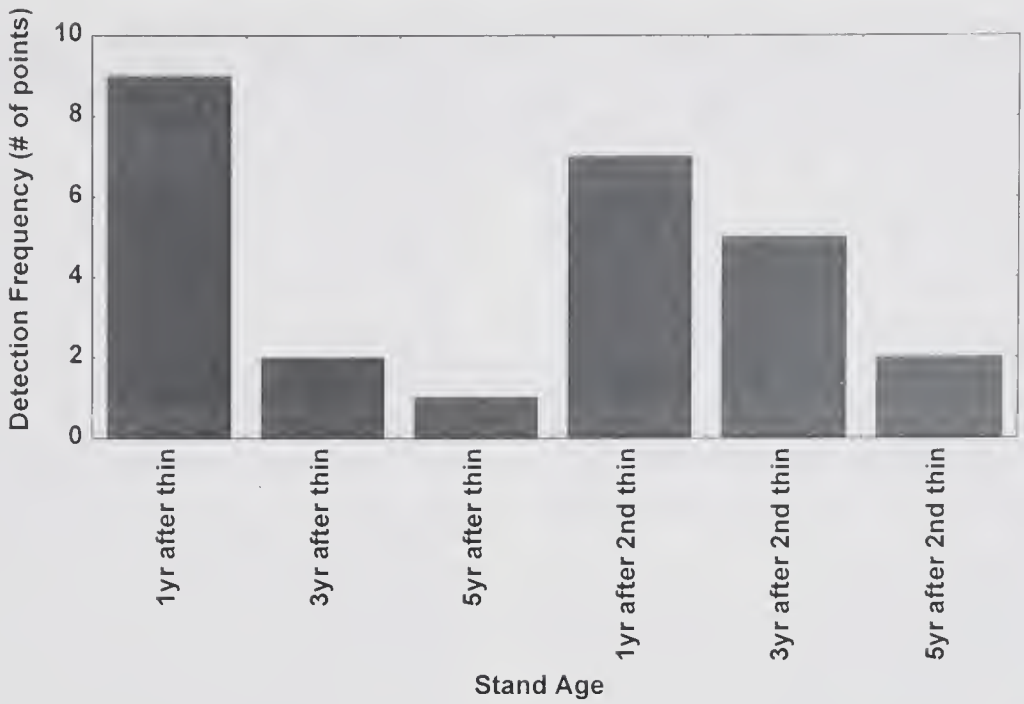

FIG. 1. Detection frequency (# of point counts) of Brown-headed Nuthatches in commercially thinned pine plantations in eastern North Carolina (n = 24 point counts for each stand type). Frequency distribution between stand ages was significantly different from an even distribution ($\chi^2_{\text{Yates correction}}$ = 12.3, df = 5, $P < 0.05$).

al. 1995), similar to the decline in nuthatches we observed following thinning.

One possible explanation for the inverse relationship between the density of understory vegetation and numbers of Brown-headed Nuthatches is that vegetation may obscure potential cavity locations. Brown-headed Nuthatch cavities are frequently excavated in relatively low positions; usually below 3.66 m (n = 309; McNair 1984). Most (68%) cavities were located in tree stumps (McNair 1984) suggesting that the potential for increasing cavity height may be limited. Regeneration of understory and groundcover vegetation was rapid in the current study such that low cavity positions could be obscured quickly, but the impact on patch use by Brown-headed Nuthatches is unknown.

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DIFFERENCES IN MIGRATORY TIMING AND ENERGETIC CONDITION AMONG SEX/AGE CLASSES IN MIGRANT RUBY-CROWNED KINGLETS

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ABSTRACT.—Ruby-crowned Kinglets, *Regulus calendula,* are small temperate zone passerine migrants that breed in conifer forests of Canada and the western United States and winter along the west coast and southern United States into Mexico. Previous studies have revealed that male kinglets precede females during spring migration and that females precede males during fall migration at various sites in eastern North America. We used mist net capture data to document sex/age structure, fat loads, and morphometrics of kinglets passing through southeastern South Dakota during spring and fall migrations from 1992–1995. Males migrated significantly earlier than females in spring; median passage dates differed by at least 8 days. These data are consistent with U.S. Geological Survey Bird Banding Laboratory records for central and eastern North America, which indicate that passage of males before females during spring migration is a widespread phenomenon. Bird Banding Laboratory data also indicate that males winter significantly farther north than females. We tested whether the differential winter distribution of the sexes could account for the differential pattern of spring migration and found that differential winter distributions do not fully account for the differential timing of spring migration between the sexes. Sex-specific migration rates do not differ over the entire spring migration route, so differences in the onset of migration apparently contribute to differential spring migration. Males migrated significantly later in the fall than females, with median dates in southeastern South Dakota differing by 7 days. We also examined whether differences in energetic condition were associated with differences in migratory timing. Visible fat scores did not differ between males and females in spring, although males had a significantly higher mean condition index (mass/wing chord). Sexes within the same age class did not differ in visible fat scores in fall, but adults tended to be fatter than juveniles, significantly so in some cases. No significant differences in condition index were apparent among sex/age classes in fall, although the adult-juvenile difference approached significance ($P < 0.09$), with adults having higher values. This tendency toward elevated fat and condition index in adults relative to juveniles in fall is consistent with more efficient foraging by adults than by inexperienced juveniles at migratory stopover sites, although differences in predation pressure or migratory routes and destinations might also be involved. *Received 12 May 1998, accepted 24 Oct. 1998.*

Differential timing of migration of sexes and/or age classes has been reported for numerous birds (see Gauthreaux 1982, Ramos 1988 for reviews). For passerine birds, males generally precede females in spring, but the timing of migration in fall is more complex and varied between sexes or age classes (see Hall 1981, Gauthreaux 1982, Francis and Cooke 1986, Ramos 1988, Nolan and Ketterson 1990, Hussell 1991, Winker and Rappole 1992). Earlier passage of males than females in spring presumably relates to advantages in territory acquisition that accrue to those individuals arriving early on the breeding grounds, regardless of whether this early arrival results from sexual differences in wintering areas, departure dates, or rates of migration (Myers 1981, Chandler and Mulvihill 1990). Differential timing of fall migration may result from differences in departure dates or rates of migration as a result of ecological or physiological factors (e.g., juvenile development, parental responsibilities, molt, fat deposition), and/or from differential distribution of age/sex classes throughout the wintering range (Gauthreaux 1982, Ketterson and Nolan 1976, Morton 1984, Prescott and Middleton 1990, Woodrey and Chandler 1997).

Ruby-crowned Kinglets, *Regulus calendula,* are small passerines breeding in coniferous or mixed coniferous-deciduous forests over most of northern and western North America and wintering throughout the western and southern United States, Mexico, and south to Guatemala (American Ornithologists' Union 1983). The winter range is apparently restricted to regions with a relatively mild winter climate (Lepthein and Bock 1976, Root 1988). Differential timing of migration in males and females has been reported from Iowa (Crim 1976) and Ontario (Fairfield and Shirokoff

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1978), but migration timing of sexes in the Great Plains has not been previously reported. In addition, male kinglets apparently winter farther north, on average, than females (Fairfield and Shirokoff 1978), but the extent to which differences in winter distribution affect differential migration is unknown. No previous study has been attempted to define the relative roles of geographic origin, departure dates, and rates of migration in shaping differential migration patterns in kinglets.

We used capture data from spring and fall migration periods from 1992–1995 in southeastern South Dakota to document patterns of migratory movement in Ruby-crowned Kinglets and to determine whether timing of migration and energetic condition differed between sexes in either season. We compared these results with banding data from the U.S. Geological Survey Bird Banding Laboratory (BBL) for central and eastern North America (east of 107° W longitude) to determine if patterns of migration between sexes in southeastern South Dakota are consistent with migratory patterns in Ruby-crowned Kinglets in eastern North America. We also tested the hypothesis that differential winter distributions could fully account for differential migratory timing.

METHODS

Collection of capture data.—Banding was conducted during spring and fall migration from 1992–1995 at four deciduous woodland study sites in southeastern South Dakota. Two sites were located in riparian habitats along the Missouri River (42° 45′ N, 97° 00′ W; and 42° 46′ N, 97° 07′ W), one study site was in a riparian woodland along the Big Sioux River (42° 45′ N, 96° 37′ W), and one study site included both riparian and upland woodlands along Brule Creek (42° 55′ N, 96° 46′ W), a tributary of the Big Sioux River. Riparian habitats along the Missouri River consisted of deciduous forest dominated by cottonwood (*Populus deltoides*), boxelder (*Acer negundo*), American elm (*Ulmus americana*), mulberry (*Morus alba*), and dogwood (*Cornus* spp.). The Big Sioux River site was dominated by boxelder, silver maple (*Acer saccharinum*), and cottonwood. The riparian forest at the Brule Creek site consisted mainly of boxelder and American elm, while the upland forest was dominated by bur oak (*Quercus macrocarpa*) with American elm and hackberry (*Celtis occidentalis*) also present. The Missouri River study sites have a generally west-east orientation, while the Big Sioux River and Brule Creek sites are oriented north-south. Extensive deciduous woodlands in this area of South Dakota, and indeed over most of the northern Great Plains, are mainly restricted to river courses (South Dakota Ornithologists' Union 1991).

Kinglets were captured using mist nets during spring (15 April–26 May) and fall (5 September–2 November) migration periods. Capture dates were chosen to coincide with the major migratory movements for Neotropical migrants, not kinglets specifically, so the distribution of capture effort did not cover the kinglet migration evenly. However, the bulk of the kinglet migration through South Dakota occurs during our capture periods (South Dakota Ornithologists' Union 1991). From 15 April through 26 May in spring and from 5 September to 5 October in fall, nets were opened daily and cycled on a 4 day rotation among the four study sites so that each study site was sampled every 4 days. Later in the fall, nets were not opened every day and most capture effort was concentrated at the Brule Creek study site. We erected 2–7 mist nets (10 m × 2.6 m, 30 mm mesh) each day, depending on weather and available personnel. Net placement at the various study sites was consistent among seasons and years. We opened the nets at sunrise and nets remained open until approximately 11:00 CST during both spring and fall migration. Upon capture we measured the bird's mass to the nearest 0.1 g with an Ohaus Model LS200 balance, unflattened wing chord to the nearest 0.1 mm, and visible fat on a scale of 0–5 (Helms and Drury 1960). Fat scoring was performed by all three authors, but we regularly checked each other on individual birds to ensure that we were scoring fat similarly. During fall migration birds were aged by skull ossification as "after hatching-year" (AHY, adults) or "hatching-year" (HY, juveniles), although this method may be inaccurate after 1 October because some hatching-year birds may complete ossification after this date (Leberman 1970, Pyle et al. 1987). Retrix shape was not an effective measure of age in our population because most birds showed an intermediate condition (Pyle et al. 1987). Sex was determined by plumage differences in both seasons. Recaptures were very rare and were not included in our analyses.

We used banding data from the BBL from 1986–1995 to determine winter distributions and timing of spring migration in males and females. Data were grouped into 5° latitude zones for comparisons. Only banding records east of 107° W longitude were used in these comparisons to eliminate populations in western North America that breed at lower latitudes and winter at higher latitudes than populations in central and eastern North America. We considered records from 1 December–29 February as winter records, and from 1 April–31 May as spring records. Banding data were provided as number of captures for consecutive 5 day periods.

To determine whether differences in winter distribution of male and female Ruby-crowned Kinglets are sufficient to account for spring migration patterns, we used a method developed by Chandler and Mulvihill (1990) to calculate a predicted pattern of differential migration based on winter distributions of the sexes.

TABLE 1. Winter (December–February) abundance of male and female Ruby-crowned Kinglets in eastern and central North America from BBL records and results of χ^2 Goodness of Fit tests for equal abundance at each latitude.

Latitude[a] (°N)	Males	Females	% Males	χ_c^2	Significance
< 25	14	14	50.0	0.04	$P > 0.05$
25–29° 59′	30	28	51.7	0.02	$P > 0.05$
30–34° 59′	169	133	56.0	4.06	$P < 0.05$
35–39° 59′	54	17	76.1	18.25	$P < 0.001$

[a] Latitudes north of 40° N had too few records ($n = 5$) to adequately assess distribution of sexes.

Chandler and Mulvihill (1990) assumed a linear change in the percentage of males in the population from the northern to the southern extent of the wintering range for their winter distribution; they predicted a linear change in the percentage of males in the population throughout migration from the first appearance to the last appearance of migrating males. They then used linear regression to calculate the predicted percentage of males throughout the migratory period and compared this regression against a linear regression of the observed percentage of males over the migratory period.

We used BBL data for wintering Ruby-crowned Kinglets to calculate a predicted differential pattern of spring migration between the sexes. The predicted percentage of males in the migratory population was calculated using the percentage of males in wintering populations from BBL data for 5° latitude zones over the entire kinglet wintering range in eastern and central North America (Table 1). We then divided the spring migratory period for males into an equal number of intervals (4 intervals at 5 days each) and assumed that the percent males during each successive 5-day interval (from first to last appearance) should equal the percent males in consecutive 5° latitude zones from north to south.

Statistics.—Median passage dates for sexes were compared by median tests (Zar 1996). Because capture effort was not evenly distributed over the entire kinglet migration period, median tests may be misleading. To control for uneven capture effort, we compared passage dates for sexes by Kolmogorov-Smirnov test for frequency distributions (Sokal and Rohlf 1995) as a function of cumulative net hours over all years pooled. Morphometrics, condition index [mass/wing chord (Winker 1995)], and visible fat scores for males and females in spring were compared by Student's *t*-test or, if sample variances were unequal (determined by *F*-test), Mann-Whitney test. In fall, morphometrics, condition index, and visible fat scores of sex/age classes were compared by one-way ANOVA, or by Kruskal-Wallis test if sample variances differed (*F*-test). Because skull ossification provides unreliable age distinction after 1 October in kinglets (Leberman 1970), fall comparisons of sex/age classes were conducted twice, excluding data after 30 September for birds with completely ossified skulls (aged AHY) and excluding all data (HY and AHY) after 30 September. If significant differences among sex/age classes were detected by ANOVA or Kruskal-Wallis tests, Student's *t*-tests or Mann-Whitney tests were used to identify which means differed with a sequential Bonferroni procedure employed for α-level adjustment to protect against inflated type 1 error rates in multiple comparisons (Rice 1989). This procedure involved six comparisons ($k = 6$) among the four sex/age classes for each variable measured (mass, wing chord, fat score, and condition index). For α-level adjustment, *P* values from individual *t*-tests for each comparison were ranked from smallest (P_1) to largest (P_6). The smallest *P* value was considered significant only if it was less than α/k (0.05/6 in this case). If P_1 was significant, then P_2 was considered significant only if less than $\alpha/k - 1$, P_3 was considered significant only if less than $\alpha/k - 2$, and so on, until the equality $P_i \leq \alpha/(1+k - i)$ was not met (Rice 1989). Once a *P* value was found to be not significant, all larger *P* values for that comparison were also considered nonsignificant.

For winter BBL data, distributions of males and females in 5° latitude zones were compared by 2-tailed χ^2 Goodness of Fit test with a null hypothesis of equal distribution (1:1) in each latitude zone. Bird Banding Laboratory data for timing of spring migration in males and females were compared by Kolmogorov-Smirnov test for frequency distribution as a function of cumulative captures during the migratory season pooled over all years (1986–1995). To determine whether winter distributions of sexes could fully account for differential migration in spring, predicted and observed percentages of males in the migratory population were compared by ANCOVA. Because neither the change in the percentage of males in the wintering population as a function of latitude nor the percentage of males in the migratory population through the spring migratory period varied in a linear fashion (Fig. 1), data for percent males were arcsine transformed prior to ANCOVA. In addition, we conducted Fisher's exact tests on observed versus predicted percent males for each 5 day interval over the spring migration of male kinglets. Statistical comparisons of mass, wing chord, condition index, and visible fat scores were conducted with Number Cruncher Statistical System (Version 4.1, Kaysville, Utah). Other statistical tests were performed with SAS (PC Version 6.03, SAS Institute 1988).

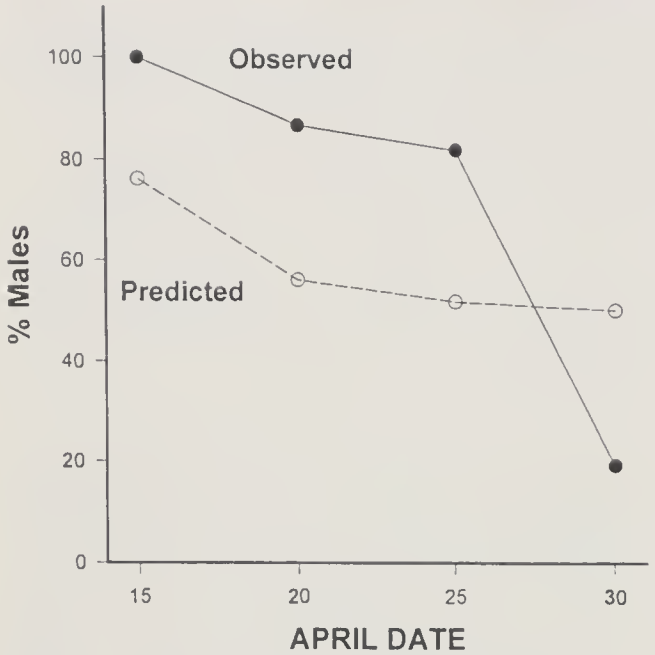

FIG. 1. Observed and predicted percentages of male Ruby-crowned Kinglets in the population during successive 5-day intervals over the spring migratory period as measured by capture data (first captures only). Predicted values were calculated based upon U.S. Geological Survey Bird Banding Laboratory data from 1985–1995 for wintering distributions of male and females kinglets east of 107° W longitude.

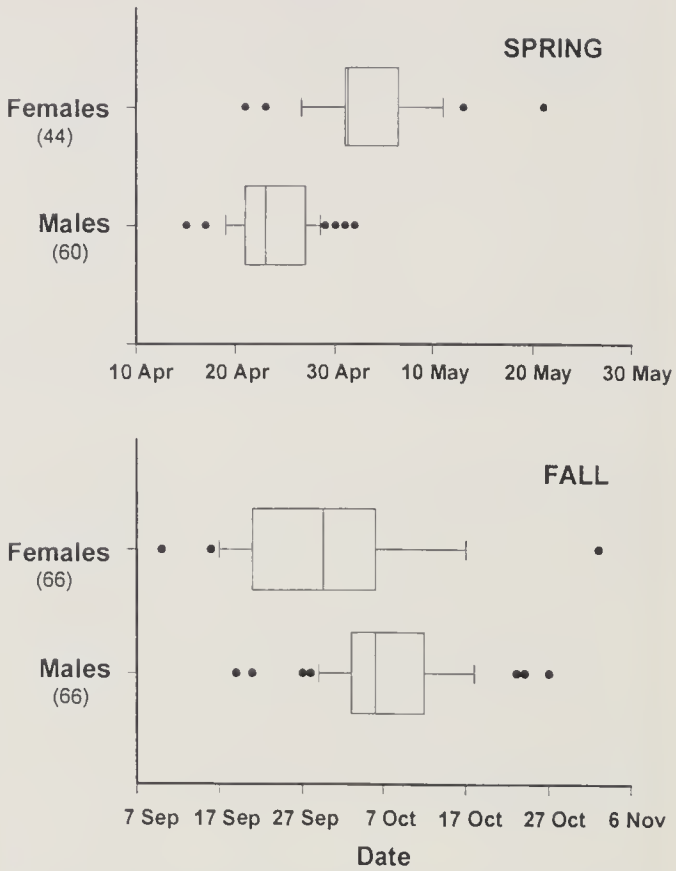

FIG. 2. Distribution of capture dates (first captures only) for male and females Ruby-crowned Kinglets during spring and fall migration. Box plots display the median (vertical line within box), the interquartile range (extent of box), the 10th–90th percentile range (extent of horizontal lines), and the data points falling below the 10th or above the 90th percentiles (dots). For spring females, the median passage date and the lower interquartile boundary were coincident on 1 May. The numbers included in parenthesis for males and females represent sample sizes for each season.

RESULTS

Southeastern South Dakota is not a part of the breeding range for Ruby-crowned Kinglets (South Dakota Ornithologists' Union 1991), so all birds in our samples were transients. Median passage dates for all years pooled for male and female kinglets in spring were 23 April and 1 May, respectively (Fig. 2). For fall migration, median passage dates for all years pooled were 29 September for females and 6 October for males (Fig. 2). Median tests indicated that males migrated significantly earlier ($\chi^2 = 45.74$, df = 1, $P < 0.001$) than females in spring and significantly later ($\chi^2 = 5.30$, df = 1, $P < 0.01$) than females in fall.

Total net hours (1 net hour = 1 net open for 1 h) were 2,081 in spring and 1,369 in fall. Our capture effort increased gradually over the spring migratory period (as days became longer) and similarly decreased gradually over the early part of fall migration (5 September–5 October). Capture effort was reduced after 5 October and only 12% of all fall net hours occurred after this date. This reduced capture effort late in fall migration may have reduced the relative number of captures of late migrating kinglets, mostly males, so the difference in median passage dates between sexes in fall that we report is probably conservative. Because capture effort was not even throughout migration periods, we tested whether frequency distributions of sexes differed as a function of cumulative capture effort. Again, these tests indicated that males migrated significantly earlier in spring (Kolmogorov-Smirnov test: $D = 0.673$, $n = 104$, $P < 0.001$) and significantly later in fall ($D = 0.425$, $n = 132$, $P < 0.001$) than females.

Data from the BBL indicated that at all latitudes males migrated significantly earlier in spring than females (Table 2). Median passage dates differed between the sexes by 10–15 days in the different 5° latitude zones. In winter, BBL data indicated that males had a significantly higher relative abundance than females at 30–35° N ($\chi^2 = 4.06$, df = 1, $P <$

TABLE 2. Median migration dates (5-day intervals) for male and female Ruby-crowned Kinglets in eastern and central North America from BBL records for April and May 1985–1996. Males migrated significantly earlier (Kolmogorov-Smirnov test: $P < 0.001$) than females at all latitudes. Sample sizes are given in parentheses.

Latitude[a] (°N)	Males	Females	*D*	*P*
30–34° 59′	6–10 April (69)	16–20 April (115)	0.333	< 0.001
35–39° 59′	16–20 April (275)	1–5 May (319)	0.566	< 0.001
40–44° 59′	21–25 April (1647)	6–10 May (1691)	0.502	< 0.001
45–50°	26–30 April (230)	6–10 May (297)	0.450	< 0.001

[a] 5° latitude zones to the south and north of those above had too few total records (≤ 27) to adequately quantify medians for each sex.

0.05) and 35–40° N ($\chi^2 = 18.25$, df = 1, $P < 0.001$), but sexes were evenly distributed south of 30° N latitude (Table 1). Thus, male Ruby-crowned Kinglets winter farther north than females.

ANCOVA revealed that slopes for equations describing observed and predicted percent males in the spring migrant population differed significantly ($F_{1,4} = 9.46$, $P = 0.037$). Least-squares regression yielded the following equations:

$$\text{arcsin Predicted \% Males} = 65.76 - 5.22(\text{Time Interval}) \quad (n = 4,\ R^2 = 0.99,\ P < 0.001)$$

$$\text{arcsin Observed \% Males} = 111.05 - 19.54(\text{Time Interval}) \quad (n = 4,\ R^2 = 0.89,\ P = 0.05)$$

where Time Interval refers to successive 5-day intervals (1–4) from first (15 April) to last (2 May) capture of migratory males. For 20–24 April a higher percentage of males was captured than predicted (Fisher's exact test, $P = 0.039$) and for 30 April–4 May a lower percentage of males was captured than predicted (Fisher's exact test, $P = 0.04$); significant differences were not detected for other intervals. These data indicate that migratory passage of the sexes during the early season is more biased toward males than expected on the basis of their wintering distribution.

Rates of migration can also be estimated for males and females by dividing the distance between two successive 5° latitude zones (assuming 1° equals 111 km) by the number of days difference between median passage dates for each zone as determined from BBL data (Ellegren 1990, Woodrey and Chandler 1997). Estimating migration rates in this manner shows that both males and females increase migration speed as they near their breeding grounds. For latitudes south of our study sites migration rates for males and females were 74 and 56 km day^{-1}, respectively, but for all latitudes overall migration speed was 83 km day^{-1} for both sexes.

Male kinglets were significantly heavier than females ($t_{102} = 5.76$, $P < 0.001$) in spring. Visible fat scores did not differ significantly between males and females in spring, but spring males had significantly longer wings ($t_{102} = 9.49$, $P < 0.001$) and significantly higher condition index (Mann-Whitney test: $Z_{102} = 3.20$, $P = 0.001$) than spring females (Table 3). When age classes were pooled by sex in fall, males were significantly heavier than females ($t_{130} = 4.80$, $P < 0.001$) and had significantly longer wings ($t_{130} = 11.79$, $P < 0.001$). Neither visible fat nor condition index differed significantly between males and females in fall when age classes were pooled.

In fall, when AHY data after 30 September were excluded from comparisons, AHY males ($t_{38} = 3.39$, $P = 0.002$) and HY males ($t_{55} = 3.93$, $P < 0.001$) were both significantly heavier than HY females. Similarly, when all data after 30 September were excluded, AHY males were significantly heavier than HY females ($t_{24} = 3.035$, $P = 0.006$). Mass did not vary significantly among other sex/age classes in fall (Table 3). Visible furcular fat scores were significantly greater in AHY females than in juveniles in fall when AHY data after 30 September were excluded from comparisons (Mann-Whitney test: $Z_{49} = 3.14$, $P = 0.002$; $Z_{35} = 2.99$, $P = 0.003$ for HY females and HY males, respectively). Likewise, when all data after 30 September were excluded from analyses, AHY females carried significantly more furcular fat than HY females (Mann-Whitney test: $Z_{34} = 2.840$, $P = 0.005$).

TABLE 3. Means (± SD) of mass, wing chord, fat class, and condition index (mass/wing chord) in migrant Ruby-crowned Kinglets. Age classes (AHY = adults, HY = hatching-year) refer to fall migrants.

Sex/age class	*n*	Mass (g)	Wing chord (mm)	Furcular fat	Abdominal fat	Condition index
Spring males	60	6.6 ± 0.6	57.7 ± 1.3	2.2 ± 1.1	2.1 ± 1.4	1.15 ± 0.10
Spring females	44	6.0 ± 0.4	55.0 ± 1.6	2.1 ± 0.9	2.1 ± 1.0	1.09 ± 0.07
Fall males						
AHY	5	6.5 ± 0.6	58.5 ± 1.5	3.2 ± 0.8	3.2 ± 0.8	1.11 ± 0.10
HY (before 1 Oct.)[a]	5	6.3 ± 0.4	57.6 ± 1.4	1.6 ± 1.1	1.6 ± 1.1	1.08 ± 0.06
HY (all data)[b]	22	6.3 ± 0.4	57.6 ± 1.2	1.9 ± 1.0	1.8 ± 1.0	1.09 ± 0.07
All males[c]	66	6.4 ± 0.4	57.7 ± 1.4	2.0 ± 1.1	2.1 ± 1.0	1.10 ± 0.07
Fall females						
AHY	15	6.1 ± 0.4	55.1 ± 1.4	2.9 ± 0.7	2.8 ± 0.7	1.12 ± 0.07
HY (before 1 Oct.)[a]	21	5.9 ± 0.4	54.8 ± 1.2	2.0 ± 0.8	2.0 ± 0.7	1.08 ± 0.06
HY (all data)[b]	36	5.9 ± 0.3	54.7 ± 1.4	2.0 ± 0.8	2.1 ± 0.8	1.08 ± 0.06
All females[c]	66	6.0 ± 0.3	54.9 ± 1.3	2.3 ± 0.8	2.3 ± 0.8	1.10 ± 0.06

[a] Data for HY birds prior to 1 October only.
[b] Data for HY birds over the entire fall season.
[c] Includes birds with completely ossified skulls after 30 September that were of indeterminate age.

Visible abdominal fat scores were significantly greater in AHY females than in HY birds when AHY data after 30 September were excluded from comparisons ($Z_{35} = 3.11$, $P = 0.002$; $Z_{49} = 2.84$, $P = 0.005$ for HY males and HY females, respectively). When all data after 30 September were excluded from comparisons, AHY females had significantly more abdominal fat than HY females ($Z_{34} = 2.695$, $P = 0.007$). The same trend occurred for AHY males, although differences were nonsignificant (Table 3). Neither furcular nor abdominal fat varied significantly between males and females within the same age class. No significant differences among age/sex classes were detected for condition index in fall, although when male and female data for each age class were pooled the adult-juvenile difference approached significance ($t_{73} = 1.74$, $P > 0.05$ when AHY data after 30 September were excluded; $t_{43} = 1.85$, $P > 0.05$ when all data after 30 September were excluded).

Wing chord did not differ significantly among age classes in fall, but males of both age classes had significantly longer wings than females when AHY data after 30 September were excluded ($P < 0.001$) and when all data after 30 September were excluded ($P \leq 0.005$, Table 3). Test statistics for between sex wing chord comparisons were: AHY males vs. AHY females ($t_{18} = 4.35$), AHY males vs. HY females ($t_{39} = 5.59$), HY males vs. AHY females ($t_{35} = 5.59$), and HY males vs. HY females ($t_{56} = 7.94$) for comparisons with AHY data after 30 September excluded. For comparisons with all data after 30 September excluded, between sex wing chord comparison test statistics were: AHY males vs. AHY females ($t_{18} = 4.35$), AHY males vs. HY females ($t_{24} = 5.99$), HY males vs. AHY females ($t_{18} = 3.23$), and HY males vs. HY females ($t_{24} = 4.59$).

DISCUSSION

Male Ruby-crowned Kinglets migrated earlier in spring than females in both southeastern South Dakota and across eastern North America (Crim 1976, Fairfield and Shirokoff 1978, BBL data). Bird Banding Laboratory data indicate that median passage dates for the latitudes of our study sites (approximately 43° N) in eastern North America are 21–25 April for males and 6–10 May for females. These dates agree very closely with median passage dates for male and female kinglets from Iowa, which occurred from 20–25 April for males and from 5–10 May for females (Crim 1976). The median date for males in southeastern South Dakota was similar to median dates in Iowa and to median dates derived from BBL data for 40–45° N latitude in central and eastern North America (Table 2). The median date for females in our study is several days earlier than the median date from Iowa and from the median date derived from BBL data for the latitudes of our study sites. However, capture effort was not quantified in Crim (1976) and was not available for BBL

data, so median passage dates may not be directly comparable.

Earlier spring passage of males than females is a common pattern among passerines, presumably because of the advantages that early arrival provides to the sex establishing territory, which among passerines is usually the male (Gauthreaux 1982, Francis and Cooke 1986). Postponing arrival on the breeding grounds until after males have established territories might be beneficial to females if they compete for mates (Francis and Cooke 1986). Moreover, because temperatures and food availability increase throughout spring in northern latitudes, late arrival on the breeding grounds might also benefit females by providing more favorable conditions for breeding. Consistent with this latter argument, male kinglets were larger (i.e., heavier and longer wings), had higher condition index, and were more cold tolerant (Swanson and Dean 1999) than females in spring.

Because juvenile Ruby-crowned Kinglets may show complete skull ossification as early as 1 October (Leberman 1970), documentation of differential migration patterns of age classes in fall is problematic. In addition, we found retrix shape (Pyle et al. 1987) to be unreliable for aging kinglets in our population. Thus, we were unable to compare passage dates for age classes during fall migration. However, males migrated significantly later than females during fall migration in southeastern South Dakota. This pattern of males migrating later in the fall than females is consistent with the observations of Fairfield and Shirokoff (1978) for Ruby-crowned Kinglets from Ontario.

Prescott (1980) found that adult female kinglets were fatter than adult males in fall in New Jersey, but sexes did not differ in fat scores during fall migration in our study. Adult kinglets in New Jersey (Prescott 1980) had a higher percentage of individuals with either no fat or heavy fat than juveniles, while juveniles had higher percentages of individuals with intermediate fat loads. In our study males were heavier than juvenile females in fall, but not adult females. Moreover, adults in our study carried more fat than juveniles in fall, significantly so for females. Woodrey and Moore (1997) reviewed several possible explanations for elevated fat levels in adults compared to juveniles during migratory stopover. These include: (1) less efficient foraging by juveniles at stopover sites because of inexperience or lower social status, (2) juveniles carry less fat to increase mobility for escape from predators because they may be more vulnerable to predation, and (3) possible differences in migratory routes or destinations affecting fattening.

Proximate factors regulating differential timing of migration among sex/age classes include differences in geographic origin, timing of the onset of migration, and rates of migration (Chandler and Mulvihill 1990). Fairfield and Shirokoff (1978) analyzed North American banding data from 1972–1975 and found that male kinglets winter farther north than females on average. Bird Banding Laboratory data from 1986–1995 also indicate that male kinglets winter farther north than females (Table 1) so different geographic origins undoubtedly contribute to differential migration of the sexes in the spring. However, passage of sexes during the early portion of spring migration is more biased toward males than expected on the basis of the differential wintering distributions. Sample sizes from BBL data for 1986–1995 for wintering populations of kinglets in eastern and central North America were relatively small, particularly south of 30° N latitude, even though kinglets regularly winter south of this latitude (AOU 1983, Ingold and Wallace 1994). Bird Banding Laboratory data indicate approximately equal numbers of males and females at southern latitudes in the wintering range, whereas females should outnumber males in the southern part of the wintering range, assuming equal sex ratios on breeding grounds. This could influence calculation of predicted percent males during the latter part of the spring migration of males, but should not affect comparisons during the early portion of the migration. Because a higher percentage of males was observed than predicted based on wintering distribution during the early part of spring migration, the small sample size from southern portions of the wintering range should not influence our conclusions that wintering distributions do not fully account for differential migration of the sexes in spring.

This suggests that males either migrate at a faster rate or initiate migration earlier than fe-

males. Calculation of spring migratory rates from BBL data revealed that male kinglets migrate at a faster pace than females south of 45° N latitude, but that rates over the entire migratory range do not differ between sexes. Thus, elevated rates of migration in males relative to females may contribute to their early arrival at our study sites, but not at higher latitudes. This suggests that the onset of spring migration is earlier in male Ruby-crowned Kinglets than in females and that this difference contributes substantially to differential spring migration of the sexes in this species.

For fall migration, where all sex/age classes presumably initiate migration from breeding grounds, differential timing of migration should reflect differences in onset or rate of migration, assuming that sex/age classes exhibit similar migration routes and that little postbreeding dispersal away from breeding sites occurs prior to southward migration. Fairfield and Shirokoff (1978) suggested that differential migration of the sexes in fall results from earlier departure of females from breeding grounds for two possible reasons. First, females are smaller and presumably less hardy than males, so they might depart before food availability and temperatures decline markedly in the fall. However, cold tolerance of male and female kinglets during fall migration through South Dakota did not differ significantly (Swanson and Dean 1999). Second, females might depart earlier than males because they winter farther south and, therefore, must travel farther. If we assume that all sex/age classes initiate migration from breeding grounds, then differential migration of sex/age classes might result not only from differences in departure, but also from differences in rates of migration (Chandler and Mulvihill 1990). Because Fairfield and Shirokoff (1978) did not directly test whether early departure or rates of migration differed between the sexes in fall, their suggestion must remain tentative. In our study males migrated later than females in fall but comparisons among age classes were confounded because juvenile kinglets could not safely be distinguished from adults after 1 October (Leberman 1970).

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SCALE-DEPENDENT HABITAT SELECTION BY AMERICAN REDSTARTS IN ASPEN-DOMINATED FOREST FRAGMENTS

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ABSTRACT.—We examined scale-dependent site occupancy of American Redstarts (*Setophaga ruticilla*) in forest fragments (2–140 ha in area) dominated by mature trembling aspen (*Populus tremuloides*) in central Alberta, Canada. Vegetation within territories, both adjacent to and away from nests, differed from vegetation in unoccupied fragments and within occupied fragments outside of territories. Territories contained higher densities of willow (*Salix* sp.), a taller shrub-layer, and lower densities of trembling aspen than other sites. Willow was the most frequently used plant species for nesting and foraging. Our results indicate that even within mature forest patches, American Redstarts select disturbed areas dominated by early successional plant species. *Received 6 March 1998, accepted 30 Aug. 1998.*

Numerous researchers have investigated habitat selection by American Redstarts (*Setophaga ruticilla*), but debate continues regarding the preferred age of forest stands used for breeding. Although most studies reported that American Redstarts prefer early successional forests (Martin 1960, Collins et al. 1982, DeGraaf 1991, Westworth and Telfer 1993, Huffman 1997), they have also been commonly found in mid- to late successional stands (Bond 1957, Ficken and Ficken 1967, Crawford et al. 1981, Morgan and Freedman 1986, Thompson and Capen 1988). Scale-dependent habitat requirements have been poorly documented for the American Redstart. Because abiotic and biotic factors may affect a species differently at various spatial scales (Bock 1987, Wiens et al. 1987), some documented differences in habitat selection may be due to scale effects. Thus, a holistic understanding of a species' habitat use patterns may require that data be collected and analyzed at several spatial scales (e.g., patch, territory, and nest site; Bergin 1992, Steele 1992, Kelly 1993). Considering that many forest patches are heterogeneous in age and structure (e.g., woody vegetation may increase in age and height from edge to interior), the investigation of scale-dependent habitat use patterns of the American Redstart could clarify the species' requirements and reconcile some of the inconsistencies in reported habitat preferences.

We studied scale-dependent habitat selection of the American Redstart in forest fragments dominated by mature trembling aspen (*Populus tremuloides*) at the northwestern edge of the species' range in central Alberta, Canada. We asked: (1) do American Redstarts occupy available forest fragments based on particular habitat characteristics (vegetation structure and composition), and (2) within an occupied fragment, do American Redstarts select territories and nest sites based on habitat characteristics?

STUDY AREA AND METHODS

The study was conducted around the Meanook Biological Research Station (54° 37′ N, 113° 20′ W) near Athabasca, Alberta, between 9 May and 6 July 1994. Upland forests in this region are primarily a mosaic of trembling aspen and white spruce (*Picea glauca*) stands which was historically created and maintained by fire (Rowe 1972). We examined eight forest fragments dominated by mature (>80 yr old) trembling aspen interspersed with patches of willow (*Salix* sp.) and alder (*Alnus* spp.). A fragment was defined as a wooded area separated from other wooded areas by more than 30 m of cropland or pasture (see Villard et al. 1995). Forest fragments varied from 2 to 140 ha (areas were calculated from 1:30,000 aerial photographs using a Placon® digital planimeter). All fragments were located within a 9-km² area and represented the range of fragment sizes available in the landscape (for details see Sodhi and Paszkowski 1997). The selection of fragments was constrained by various factors including stand age, access, presence of cattle, and landowner cooperation.

Each fragment was flagged into 100 × 100 m grids and was surveyed three times to locate redstart territories. During surveys, we walked along the flagged gridlines and visually located all redstarts (primarily by following singing males). Locations of redstarts, along with characterization of individual plumage patterns (see below) were recorded on a gridded map.

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Unoeeupied fragments were surveyed again in late June by playing American Redstart territorial songs for 2 min at 50-m intervals and waiting 5 min for a response. No new individuals were detected during these surveys. Individual males were identified based on location of territory and on patterns of plumage coloration on the breast, abdomen, neek, and head (Sherry and Holmes 1989, Lemon et al. 1992). Because second year male redstarts can differ from older males in habitat seleetion (e.g., Sherry and Holmes 1989, Hunt 1996), we colleetcd habitat data only for males in full adult plumage.

The composition of vegetation was measured within territories, outside of territories, adjacent to the nest tree, and in unoecupied habitat fragments. We sampled in early to mid-July after the breeding season. Vegetation plots were located at random with the following exceptions: plots associated with nest trees were dictated by nest location and plots associated with territories were always plaeed at least 10 m inside a boundary. A total of 88 vegetation plots were sampled: 33 within 13 territories, 17 outside of territories but within 4 occupied fragments, 17 immediately around 17 nest trees, and 21 plots in 4 unoeeupied fragments.

We sampled vegetation using a modification of the circular sample-plot method (James and Shugart 1970). For each of the four site types, we recorded four sets of information: (1) tree (woody plants more than 1.75 m tall) species, number, height (using a elinometer), and diameter at breast height (using a dbh measuring tape) within a 22.4 m diameter circular plot, (2) shrub (woody plant less than 1.75 m tall) species, number, and maximum height within a 10 m diameter circular plot, (3) presence/absence of canopy (above 5 m) at 20 random points within the 22.4 m diameter plot using a 4 cm diameter ocular tube, and (4) presence/absence of ground cover at the same 20 random points using the ocular tube. The last two sets of information gave a measure of relative canopy and ground eover, respeetively.

We used Principal Components Analysis (PCA) to compare vegetation eomposition within and among the four site-types (CANOCO; ter Braak 1991) for all 88 plots. Principal Components Analysis is recommended and frequently used for analysis of habitat data (Doncaster et al. 1996, Hunt 1996). The 27 vegetation variables recorded for eaeh plot (Table 1) were square-root transformed to approximate a normal distribution. A univariate analysis, Kruskal-Wallis test, was used to determine if PCA seores for the first two ordination axes differed among site types. If the Kruskal-Wallis test was signifieant ($P < 0.05$), Multiple Comparisons tests were performed to determine which characteristies differed (Siegel and Castellan 1988). All statistical tests were done using STATVIEW version 4.1 on a Macintosh-eompatible computer.

RESULTS

Redstarts occurred in four forest fragments (2, 50, 107 and 140 ha in area) but were absent from four others (4, 6, 9 and 32 ha). Principal Components Analysis based on vegetation characteristics clearly grouped and separated unoccupied plots from plots within territories (Fig. 1). Loadings of vegetation variables on PCA Axis I indicated that unoccupied fragments and areas outside of territories within occupied fragments contained larger trees and higher densities of trembling aspen, accompanied by prickly wild rose (*Rosa acicularis*), red-osier dogwood (*Cornus stolonifera*), and honeysuckle (*Lonicera* spp.) (Table 1). Areas within territories were characterized by high densities of willow (both trees and saplings), cherry (*Prunus* sp.), saskatoon berry (*Amelanchier alnifolia*) and balsam poplar (*Populus balsamifera*) saplings, as well a tall shrub-layer (loadings on Axis 1, Table 1). Scores on Axis I differed significantly among site types ($KW = 42.51$, df = 3, $P < 0.001$). There was no significant difference between nest sites and plots within territories (Multiple Comparisons test: $P > 0.05$), but both differed significantly from plots in unoccupied fragments and plots outside of territories within occupied fragments (Multiple Comparisons tests: $P < 0.05$). Plots in unoccupied fragments and those outside of territories in occupied fragments had similar PCA I scores (Multiple Comparisons test: $P > 0.05$).

Nest sites were associated with high densities of white birch (*Betula papyrifera*, both trees and saplings), willow, cherry, and balsam poplar saplings, as well as *Viburnum* spp., which contributed to a tall shrub layer (high scores and loadings on Axis II). Nest sites were also clustered on PCA Axis II ($KW = 17.79$, df = 3, $P < 0.001$). On this axis, only scores for nest sites differed significantly from scores for plots from unoccupied fragments (Multiple Comparisons tests, $P < 0.05$). However, there was similarity in vegetation characteristics in some plots within territories and those at nest sites (Fig. 1).

DISCUSSION

Principal Components Analysis and subsequent univariate analyses indicate that redstarts did not establish territories randomly within or among forest patches, but based their occupancy on vegetation characteristics. A high abundance of willow was a particular-

TABLE 1. Loadings of vegetation variables on the first and second Principal Components axes (PC I and PC II).

Variables	PC I	PC II
Eigenvalues	0.42	0.12
Variation explained (%)	42.4	11.1
No. trees (woody plants > 1.75 m tall)		
Willow (*Salix* sp.)	−121	−289
Trembling aspen (*Populus tremuloides*)	338	−654
Balsam poplar (*P. balsamifera*)	38	19
White birch (*Betula papyrifera*)	−101	556
Alder (*Alnus* spp.)	29	195
White spruce (*Picea glauca*)	28	133
Tree sizes		
Mean tree height (m)	−95	−68
Mean dbh (mm)	203	318
No. shrubs (woody plants 0.5–1.75 m tall)		
Red-osier dogwood (*Cornus stolonifera*)	224	106
Wild gooseberry (*Ribes oxyacanthoides*)	−55	103
Wild red raspberry (*Rubus idaeus*)	75	−229
Honeysuckle (*Lonicera* spp.)	183	−418
Prickly wild rose (*Rosa acicularis*)	996	81
Snowberry (*Symphoricarpos* spp.)	203	88
Caragana sp.	−74	−121
Viburnum spp.	91	522
Prunus spp.	−223	448
Saskatoon berry (*Amelanchier alnifolia*)	−139	−5
Maple sapling (*Acer* sp.)	−11	0
Balsam poplar sapling	−122	266
Willow sapling	−158	380
Trembling aspen sapling	39	196
White birch sapling	−119	769
Alder sapling	142	172
Shrub height		
Mean maximum shrub height (mm)	−206	563
Cover[a]		
Canopy	−97	177
Ground	−37	5

[a] See Methods for estimation of these variables.

ly distinctive feature of areas within territories and around nest sites. Willow was the most frequently used foraging site (mean ± SE = 65.8 ± 8.9% of observation time, n = 13 males for which we had at least 10 min of observations) and nesting site (13 of 20 nests; Sodhi and Paszkowski, unpubl. data). Areas within territories and nest sites were characterized not only by willows, but also by a tall shrub layer in general. American Redstarts have been found to be positively associated with shrub cover in Minnesota (Huffman 1997). The extra cover and structural complexity provided by taller shrubs may have protected nests from predation or parasitism and thus enhanced reproductive success (Morris and Lemon 1987). Nest sites also supported higher densities of white birches, which have wider leaves than willows and may improve nest cover. In our study area, only 18% (n = 22) of the nests were parasitized by Brown-headed Cowbirds (*Molothrus ater*) and only 18% (n = 22) were depredated (Sodhi and Paszkowski, unpubl. data). Both nest parasitism and depredation rates at our sites were relatively low compared to other studies (e.g., Freedman 1929, Sherry and Holmes 1992). The structural complexity of understory vegetation in earlier successional stages could offer appropriate nest protection for redstarts.

Certain plant species, most notably trembling aspen, were underrepresented on sites

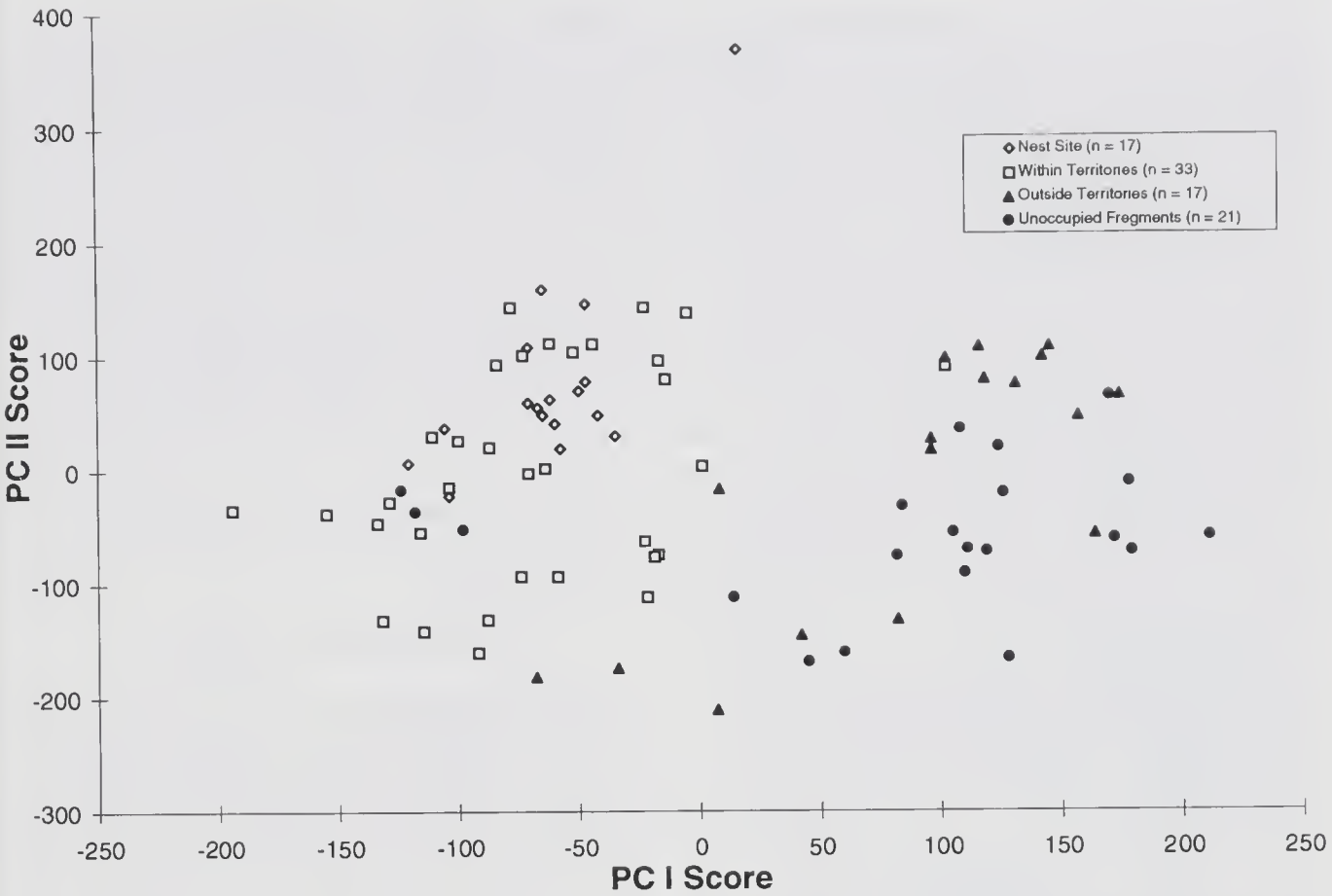

FIG. 1. Comparison of sites occupied and unoccupied by American Redstarts based on the first two Principal Component scores of plot vegetation. The Principal Components are based on 27 vegetation variables collected from 88 plots. Note: one plot near a nest was the only plot dominated by conifers and it contained little undergrowth, therefore it is distinct from all other plots.

occupied by redstarts. The lack of use of habitat dominated by common, and even dominant, tree and shrub species at both the scale of the forest patch and the territory may be related to constraints imposed on redstart foraging behavior by the leaf and branch morphology of these plant species (Holmes et al. 1978, Sedgewick and Knopf 1992). The exclusion and inclusion of certain shrub species on redstart territories could also be an artifact of their co-occurrence with overstory dominants, especially trembling aspen. The canopy forming woody species associated with habitat used by redstarts, i.e., willow and white birch, are all species typically found on wetter sites in central Alberta (Rowe 1972). Thus, it is also possible that redstarts were choosing locations in this relatively dry landscape that had higher soil moisture levels and were therefore more productive in terms of plant and invertebrate biomass (Adams and Morrison 1993). Our surveys showed that even within stands dominated by mature trembling aspen, redstarts prefered areas that supported more willows, which are typically early successional species. The presence of thickets of willow and other shrubs in these stands might be maintained by periodic localized flooding resulting from vernal soil saturation following heavy snow cover or from beaver activity (Sodhi and Paszkowski, pers. obs.).

American Redstarts are abundant in harvested aspen forests in Minnesota (Hoffman 1997). Other studies also show that redstarts attain maximum densities in stands in early successional stages of different forest types (DeGraaf 1991, Westworth and Telfer 1993, Hunt 1996). It might be argued, based on patterns reported for some other passerines (Vickery et al. 1992), that although redstarts occur at high densities in early successional forests, they reproduce poorly here compared to mid- to late successional forests. We found that 90.6% (n = 32) of older adult redstart males were paired in our study area in 1994 (Sodhi, unpubl. data); this figure is similar to

values for older males in various successional forests and in a continuous forest tract in New Hampshire (Sherry and Holmes 1989, Hunt 1996). Assuming that male pairing success is correlated with reproductive success, pockets of disturbed, productive early successional vegetation nested within mature forest stands may offer good breeding conditions for redstarts.

Every avian habitat can be represented as a spatially based hierarchy that ranges from the level of landscape to nest site. The behavioral decision-making processes behind habitat use can be related to these hierarchical habitat units (Kolasa 1989, Kotliar and Wiens 1990). Studies of scale-dependent habitat selection have revealed that the decision-making process varies among species and can sometimes operate at multiple scales within a single species (Bergin 1992). For example, Black-throated Blue Warblers (*Dendroica caerulescens*) were more selective at the habitat patch (or stand) level than at the territory level (Steele 1992). In contrast, habitat selection in Dusky Flycathers (*Empidonax oberholseri*) was primarily based on nest-site characteristics rather than on territorial features (Kelly 1993). In our study, habitat selection by American Redstarts operated most clearly at the territory level. Males defended areas of forest with a distinct plant composition and structure. Habitat selection at the territorial level was manifested, in turn, at the next higher spatial scale, as males did not occupy fragments that contained insufficient appropriate vegetation. At the finest spatial scale, evidence for nest site selection was present but relatively weak. Nest sites were not significantly different from other locations within territories, possibly because the willows and other tall shrubs used as foraging sites also offered good nest protection.

Some question remains as to whether birds actually differentiate between potential territories based on the environmental parameters that researchers perceive to be important (Morse 1989). Most authors agree however, that, at some level, territory establishment is a behavioral response to certain vegetation characteristics (Maurer and Whitmore 1981, Smith and Shugart 1987, Parrish and Sherry 1994). We concur that American Redstarts in central Alberta establish territories within a definable type of vegetation that appears to offer appropriate conditions for successful foraging and nesting. Based on our research, as well as previous studies, redstarts appear to prefer early successional forest stands or disturbed sites embedded within older stands. However, with correlative data, it remains possible that redstarts choose sites based on soil moisture or food availability, which are in turn associated with particular vegetation characteristics. In light of reported population declines for the species in parts of its range (Sauer et al. 1996), the value of such habitats should be assessed on a regional basis and their use by redstarts integrated into conservation strategies.

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FEMALE MATE CHOICE IN NORTHERN CARDINALS: IS THERE A PREFERENCE FOR REDDER MALES?

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ABSTRACT.—I tested whether female Northern Cardinals (*Cardinalis cardinalis*) associated with redder males in two laboratory experiments, one using males with unaltered plumage and the other using males with plumage altered by a lightened or reddened treatment. Females exhibited no preference for redder males. Given the long duration over which pair formation can occur in natural populations and the importance of territory quality to reproductive success, a female may choose a mate based on other morphological characteristics or aspects of his territory rather than on only red coloration. *Received 27 May 1998, accepted 22 Oct. 1998.*

Ornate plumage characteristics in birds are generally assumed to have arisen through sexual selection and, specifically, through female mating preferences or competitive interactions between males (Darwin 1871, Andersson 1994). A growing number of studies has demonstrated that females prefer males with brighter coloration (Hill 1990, Sætre et al. 1994, Sundberg 1995) as well as with other exaggerated plumage characteristics, such as longer crests (Jones and Hunter 1993) and longer tails (Andersson 1982, 1992; Møller 1988, 1992; Evans and Hatchwell 1992).

Northern Cardinals (*Cardinalis cardinalis*) are highly dichromatic. Males vary from orange to scarlet red. Male coloration varies both in overall hue and in evenness of breast coloration. In contrast, females are primarily a light brown but have small and variable amounts of red in the crest and breast; all females also have red coloration on the wings and tail.

In addition to being highly dichromatic, cardinals are territorial and socially monogamous. Males feed females substantially during nest construction, a time coinciding with egg production (Kinser 1973). Males also feed nestlings at higher rates than do females (Filliater and Breitwisch 1997, but see Linville et al. 1998). Because coloration derived from carotenoids is dependent on diet in birds (Goodwin 1950, Hill 1992), red coloration in cardinals could signal information to the female regarding a male's foraging abilities, age, or overall phenotypic quality.

In this study, I address whether female preferences may account for the maintenance of red coloration in male Northern Cardinals. I used two laboratory experiments to test whether female cardinals preferred to associate with redder males during the breeding season.

METHODS

The experiments were conducted on the Cornell University campus, Ithaca, New York, from mid February through April 1995. Males and females used in the experiments were captured between 14 January and 16 April 1995 using baited traps and mist nets at 6 sites within Tompkins County, New York (42° N, 76° W). Individuals were marked uniquely with one color band. Because previous studies have demonstrated that red color bands can influence behavior of individuals in other species (Burley et al. 1982, Hagan and Reed 1988, Metz and Weatherhead 1991), I did not use red or orange color bands.

Prior to trials males were housed in two indoor flight aviaries (3.6 × 3.6 × 3.0 m) with skylights and incandescent lighting synchronized to dawn and dusk. Females were housed in a similar third aviary (5.2 × 3.6 × 3.0 m). Aviary rooms were both visually and acoustically isolated from each other. The temperature of each aviary ranged between 10 and 12° C. Food and water were provided *ad libitum*.

Measuring coloration.—To measure male coloration, I used methods described elsewhere (Wolfenbarger in press). Briefly, I used the color chip series of the Methuen Handbook of Color (Kornerup 1967) to quantify breast coloration of males. The color chip series provides a measure of three components of color: hue, tone, and intensity. The hue component ranked color on a scale from yellow (5) to intense red (11). The tone component quantified the amount of black present [1 (all black) to 6 (none)], the intensity component indicated the degree of saturation of pigment [from little (1) to complete (8)]. I used a grid that divided the breast into eight 1 × 4 cm rectangles and

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TABLE 1. Male color and morphology differences in male cardinals used in natural trials.

	Relative color score		
	Lower $\bar{x} \pm$ SD (n)	Higher $\bar{x} \pm$ SD (n)	Z (P)[a]
Bright breast hue	73.9 ± 7.0 (8)	81.7 ± 4.3 (8)	2.81 (0.005)
Dull breast hue	65.9 ± 6.4 (8)	71.9 ± 4.0 (8)	2.81 (0.005)
Bright breast intensity	62.9 ± 0.9 (3)	63.2 ± 0.6 (3)	—[b]
Dull breast intensity	61.1 ± 3.1 (7)	62.7 ± 0.9 (7)	2.64 (0.008)
Morphological traits (in mm):			
Tarsus length	24.3 ± 0.7 (10)	24.1 ± 1.0 (10)	0.82 (> 0.05)
Crest length	36.8 ± 3.5 (10)	35.8 ± 1.9 (10)	0.46 (> 0.05)
Tail length	99.9 ± 5.0 (10)	98.4 ± 3.7 (10)	0.46 (> 0.05)
Black bib length	19.8 ± 4.6 (10)	20.2 ± 4.3 (10)	0.65 (> 0.05)
Black bib width	21.8 ± 1.1 (10)	22.0 ± 1.1 (10)	0.46 (> 0.05)

[a] Z-value is from Wilcoxon matched pairs signed rank test.
[b] In 7 trials, male scores for bright breast intensity were identical.

placed it immediately posterior to the black bib and measured coloration in each of these regions. Because male cardinals often had clumps of orange, yellow, or even tan feathers interspersed within a background of red feathers, I recorded the highest ("Bright" breast score) and lowest color score ("Dull" breast score) for hue, tone and intensity in each of the 8 regions. For all of these components a higher score indicates a redder or brighter color. Among the birds I used, there was greater variation among males in the color of dull regions relative to bright regions (Wolfenbarger, in press). I tested the repeatability of the color scoring method by using specimens in the Cornell Vertebrate Collections, and found the method to be highly repeatable (Wolfenbarger 1996).

For analyses of the association between measures of female association and male coloration, I summed each component of color (i.e., hue, tone, intensity) for the eight regions and used separate scores for the bright and dull color measurements. In this experiment, all males except two exhibited the maximum tone scores possible for both bright and dull breast measurements; therefore, the relationship between color tone and female association was not tested. Similarly, there was very little variation in bright breast intensity. Therefore, I used three variables: bright breast hue, dull breast hue, and dull breast intensity to characterize male coloration.

Although other studies have created a composite score from color chips (Linville et al. 1998), I used these components separately for two reasons. Hue and intensity were not consistently correlated in this population of cardinals (Wolfenbarger 1996), and combining these scores would result in identical scores for males that actually had different hue and intensity scores. Second, the relative importance of hue, intensity and tone for color perception of cardinals is not known. Any weighting of these components becomes problematic for the interpretation of negative results since one obvious alternative would be that the weighting factor might be incorrect.

Morphological measurements.—I measured the following on males: tarsus length, tail length, crest length, maximum length of black bib (after Møller 1987), and width of black bib. All were measured to the nearest 0.1 mm except tail length which was measured to the nearest 0.5 mm.

Experiment 1: natural plumage trials.—Ten trials were conducted to test whether females spent more time with males having higher natural plumage scores. Males and females in each trial were captured at least 4 km apart to reduce the possibility that males and females had interacted prior to the experiment. Males and females were tested in the order that they were captured from the field so that males spent similar lengths of time in captivity (approximately 7 days for natural trials and 18 days for manipulated trials), but within a trial males and females had spent similar amounts of time in captivity. No apparent change in behavior was associated with when males and females were captured or how long they spent in captivity.

In each trial males differed primarily in hue scores. Within a trial males differed significantly in bright and dull breast hue (Wilcoxon matched-pairs test: Bright hue: $Z = 2.81$, $P < 0.05$; Dull hue: $Z = 2.81$, $P < 0.05$; Table 1). There were also significant but small differences in dull breast intensity between males in a trial ($Z = 2.64$, $P < 0.05$; Table 1). The lack of differences in bright breast intensity (Table 1) reflects the limited natural variation of breast intensity in male cardinals. I analyzed bright and dull breast measurements separately because male rankings based on bright and dull measurements were not identical.

Trials were conducted in a rectangular experimental aviary (5.0 × 1.4 × 1.75 m) divided by netting into three main compartments. Males were placed at opposite ends of the aviary and a female was placed in the center compartment (2.5 × 1.4 × 1.75 m). The female compartment was divided into three equal areas so that females could associate with either male or spend time in a middle area where she could not interact visually with either male. Opaque barriers within the female area were used to divide the compartment. These prevented a male from observing a female in-

TABLE 2. Male color and morphology differences in male cardinals used in manipulated trials.

	Lightened male $\bar{x} \pm$ SD (n)	Reddened male $\bar{x} \pm$ SD (n)	Z (P)[a]
Color score before manipulation:			
Bright breast hue	75.7 ± 7.4 (10)	80.5 ± 6.5 (10)	1.89 (0.059)
Dull breast hue	68.9 ± 4.9 (10)	70.9 ± 3.5 (10)	1.99 (0.046)
Bright breast intensity	63.0 ± 0.7 (10)	63.1 ± 0.9 (10)	0.30 (> 0.05)
Dull breast intensity	61.5 ± 3.1 (10)	62.3 ± 0.9 (10)	0.34 (> 0.05)
Color score after manipulation[b]:			
Bright breast hue	72.9 ± 5.4 (9)	86.1 ± 4.3 (9)	2.69 (0.0072)
Dull breast hue	66.6 ± 6.4 (8)	77.3 ± 4.8 (8)	2.52 (0.011)
Bright breast intensity	62.8 ± 0.9 (5)	63.8 ± 0.7 (5)	0.68 (> 0.05)
Dull breast intensity	61.2 ± 0.9 (9)	63.0 ± 0.8 (9)	2.69 (0.0072)
Morphological traits (in mm):			
Tarsus length	24.0 ± 0.9 (10)	24.4 ± 0.8 (10)	0.83 (> 0.05)
Crest length	35.4 ± 2.5 (10)	37.1 ± 2.9 (10)	1.17 (> 0.05)
Tail length	99.7 ± 4.3 (10)	98.6 ± 4.5 (10)	0.35 (> 0.05)
Black bib length	20.4 ± 4.1 (10)	19.6 ± 4.8 (10)	0.56 (> 0.05)
Black bib width	21.7 ± 0.9 (10)	22.1 ± 1.3 (10)	0.82 (> 0.05)

[a] Z-value is from Wilcoxon matched pairs signed rank test.
[b] Males that have identical scores are not included in means of color scores after manipulation.

teracting with the male on the opposite side, but did not restrict female movement. I considered a female as interacting with a male when she spent time in the area adjacent to the male compartment as opposed to the center area. To minimize the possibility of side preferences, all aspects of the male compartments as well as the female compartment were symmetrical. A single perch was provided in each male compartment and three perches in the female compartment, one in each area. Food and water were provided *ad libitum* in each male compartment and in the middle area of the female compartment.

Each trial lasted 29 hours. For each trial a female was placed in the experimental aviary for a one hour acclimation period without the presence of males. A male was introduced to each side of the aviary and the experiment proceeded for 26 hours. At the end of 26 hours, the positions of the two males were switched and the female interacted with males for an additional two hours.

Females were videotaped during four different observation periods: (1) for one hour with no males present (Pretrial Period), (2) for the first two hours (0 Hour Period) after introduction of the males, (3) from 24–26 hours after introduction of the males (24 Hour Period), and (4) from 26–28 hours of the trial (Reversed Period). In sum, each female was taped for 6 hours with the two males present and for one hour prior to the introduction of males. After completion of a trial, males and females were returned to their respective aviaries.

Experiment 2: manipulated plumage trials.—The 30 individuals used in the natural plumage experiment were also used in the manipulated plumage experiment, but within each experiment individuals were used only once. Males and females for each trial were unfamiliar with each other because they were housed in different aviaries prior to the trial and were introduced in novel combinations for the two experiments. For each pair of males in a manipulated trial, one was randomly assigned to a reddened plumage treatment and the other to a lightened plumage treatment. Trials proceeded as in experiment one. At the conclusion of the manipulated trials, all individuals were released at the original site of capture.

Plumage manipulation methods.—Prior to the manipulation, males were anesthetized with 1.5 mg/kg of Midazolam injected into the pectoralis muscle. This dosage induced a state of light anesthesia: males closed their eyes but opened them in response to external stimuli such as having a wing extended. No mortality was associated with using the anesthesia.

For the "reddened" treatment, a mixture of 1 part Divina 20 Volume Creme Developer and 3 parts Clairol Professional Hi Power Tint 670® was placed on the feathers for 25 minutes. A "lightened" treatment consisted of applying Clairol Professional 7th Stage Creme Hair Lightener mixed with Divina 20 Volume Creme Developer in a 1:1 mixture to the feathers for 25 minutes. In both treatments males were rinsed and were dried with a hair dryer. The males were alert within an hour of the injection and were released back into an aviary within 2 hours. Trials were conducted at least four days after the males were manipulated.

Manipulated plumage coloration scores.—Although treatments were assigned randomly, plumage hue scores before the manipulation were significantly higher for males in the reddened treatment group (Wilcoxon matched-pairs test: Natural bright hue: $Z = 1.89$, $P = 0.06$; Natural dull hue: $Z = 1.99$, $P < 0.05$; Table 2). There was no significant difference in the intensity scores prior to the manipulation (Natural bright intensity: $Z = 0.30$, $P > 0.05$, Natural dull intensity: $Z = 0.034$, $P > 0.05$; Table 2). After plumage manipula-

tions, differences between hue scores for reddened and lightened treatment groups were significant (Manipulated bright hue: $Z = 2.69$, $P < 0.05$, Manipulated dull hue: $Z = 2.52$, $P < 0.05$; Table 2). Males in the reddened treatment had significantly higher intensity for the dull breast measurement but not for the bright measurement (Manipulated bright intensity: $Z = 0.68$, $P > 0.05$; Manipulated dull intensity: $Z = 2.69$, $P < 0.05$; Table 2). Little variation in manipulated tone scores existed: all except two individuals had the maximum possible tone scores. Reflectance spectra (from 280–750 nm) of manipulated plumage were within the range of natural variation in plumage reflectance that occurs at these wavelengths (Wolfenbarger, unpubl. data). As in experiment one, dull and bright breast measurements were analyzed separately.

Analyses of experiments.—For the periods videotaped, the time a female spent in each area of the experimental aviary was measured either during the trial via a monitor connected to one camera or after the trial from the videotapes. The monitor was located in a room visually and acoustically isolated from the experimental aviary. For each sampling period, I determined the number of trials in which the female spent more time with the male having the higher color score for each period videotaped (0 Hour, 24 Hour, Reversed). I used the 0 Hour and 24 Hour samplings to assess female preferences and the pretrial and reversed sampling periods to assess whether females had site preferences in the aviary.

For the 0 Hour and 24 Hour periods, I used a one-tailed binomial test to determine whether the number of trials in which a female spent more time with the redder/brighter male was significantly greater than expected by chance (50%; Conover 1980). The test statistic T refers to the number of trials in which the female spent more time with the male with the higher color score (Conover 1980).

Because males were randomly assigned to trials, there were trials in which hue or intensity scores were identical. I eliminated these from analyses because neither male was redder or brighter using my measurements. I also eliminated sampling periods in which the difference in amount of time spent with males was less than 2 minutes (i.e., the female showed no preference for a particular male).

Among trials, differences in male coloration scores varied widely (range in differences: bright breast = 0–21, dull breast hue = 0–24, dull breast intensity = 0–8). Females may exhibit strong preferences (as measured by time spent with male) when differences between male coloration are large; whereas females may spend equal amounts of time with males whose color scores are similar. I used regression analysis to test whether the magnitude of the difference in color was related to the difference in the time a female spent with a particular male. In particular, I tested whether there was a positive relationship between the difference in color scores between the two males and the difference in the amount of time spent between the two males in the 0 Hour and 24 Hour sampling periods (Wilkinson et al. 1992). Because the predicted difference in the amount of time spent with males of the same color is zero, the regression line was forced through the origin.

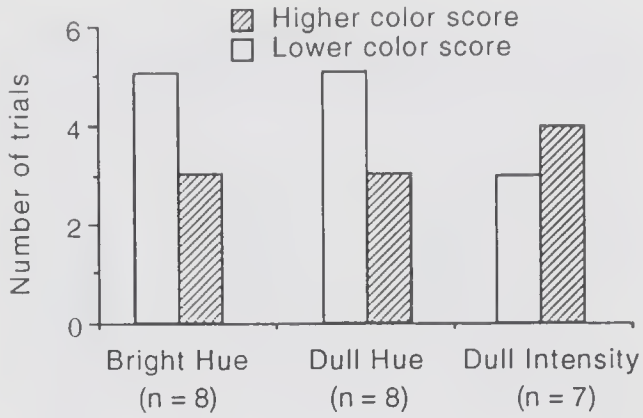

FIG. 1. Number of natural trials in which female spent more time with male having lower or higher color score during the 0 Hour Sampling period (Binomial test: all $P > 0.05$).

I tested whether females exhibited two types of potential site preferences: (1) a general preference among females for either the east or west side of the experimental aviary or (2) the likelihood that an individual female stayed on the same side of the aviary between consecutive sampling periods. I used the pretrial and reversed periods to assess the consistency of females' preferences for a particular side or male. Two-tailed binomial tests were used to determine whether females remained on the same side of the aviary between subsequent sampling periods in more than half of the trials (Conover 1980). I used a sequential Bonferroni adjustment for multiple comparisons (Rice 1989) because I used both dull and bright breast measures in analyses. A Wilcoxon matched pairs signed rank test was used to compare morphological variables between paired males (Wilkinson et al. 1992).

RESULTS

Natural and manipulated plumage experiment.—Of the 59 observation periods during the two experiments, females spent an equal amount of time (± 2 min) with both males in only 7 periods. During the remaining 52 periods, females spent an average of 45.8 (SE = 4.0) minutes more with one male than the other (range = 12–110 min, total possible = 120 min).

In the 0 Hour and 24 Hour sampling periods, females were as likely to associate with the relatively dull males as with brighter, redder males (Fig. 1, binomial test: 0 Hour: T Bright hue = 3, $P > 0.05$, $n = 8$; T Dull hue = 3, $P > 0.05$, $n = 8$; T Dull Intensity = 4, $P > 0.05$, $n = 7$; 24 Hour: T Bright hue = 5, $P > 0.05$, $n = 9$; T Dull hue = 3, $P > 0.05$,

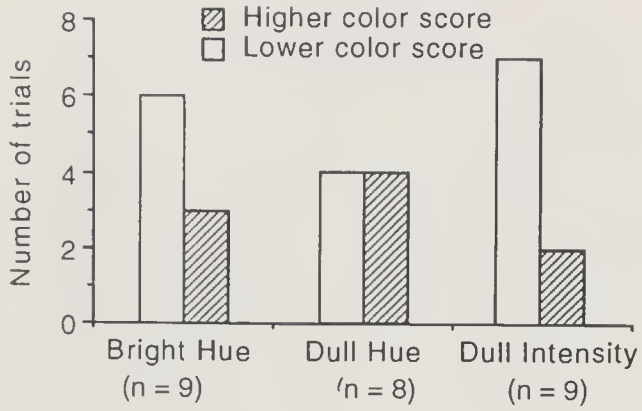

FIG. 2. Number of manipulated trials in which female spent more time with males having lower or higher color scores during the 0 Hour Sampling period (Binomial test: all $P > 0.05$).

$n = 9$; T Dull Intensity = 6, $P > 0.05$, $n = 7$). Similarly, in the manipulated plumage trials where color differences between males were greater, females did not consistently associate with males having higher coloration scores (Fig. 2; binomial test: 0 Hour: T Bright hue = 3, $P > 0.05$, $n = 9$; T Dull hue = 4, $P > 0.05$, $n = 8$; T Dull intensity = 2, $P > 0.05$, $n = 9$; 24 Hour: T Bright hue = 3, $P > 0.05$, $n = 9$; T Dull hue = 4, $P > 0.05$, $n = 8$; T Dull intensity = 2, $P > 0.05$, $n = 9$).

The power of binomial tests at the critical value is 95% at sample sizes of 8 and 9, and 70% with a sample size of 7. However, the power of all of these tests at the *P*-values of the results is less (25–36%) because of the small effect observed in the experiments. Results from at least 150 trials would be needed to find significant differences with such a minor effect (Conover 1980).

Magnitude of color differences and female association.—Within trials of both experiments, males varied widely in color differences, and it is possible that females only associated with redder or brighter males when color differences were large. If so, then the difference between coloration of males should be positively related to the difference in time a female spent with males within a trial. In contrast to this prediction, there were no positive or significant relationships between color score differences and differences in time spent with males in a trial for the natural or manipulated experiment during the 0 Hour and 24 Hour periods. In fact, all of the slopes were near zero or negative (range of $b = -0.36$ to 0.08, $n = 10$, all $P > 0.05$). Therefore as color differences between males increased, females did not spend a greater amount of time with redder or brighter males.

Female behavior in the experimental aviary.—Males and females rapidly adjusted to the experimental aviary and females spent the majority of time during trials on the three perches rather than on the floor or netting. Typically within the first 15 minutes after males were introduced, females had visited each of the side compartments. Singing occurred in 7 of the 10 natural trials and 8 of the 10 manipulated trials, but I was unable to determine from the videotapes which male (or female) sang. In any one trial singing occurred for less than 5 minutes. When adjacent to a male compartment, females sat on perches for relatively long times but regularly interrupted these periods by flights back and forth between and within the two side male compartments. Such flights also occurred in the pretrial periods.

Site preferences by females.—Females did not spend more time consistently on the east or west side of the experimental aviary (Wilcoxon test, two-tailed: natural trials: Pretrial $Z = 1.13$, $P > 0.05$, $n = 10$, 0 Hours $Z = 0.06$, $P > 0.05$; 24 Hours $Z = 0.05$, $P > 0.05$; Reversed $Z = 1.07$, $P > 0.05$; manipulated trials: Pretrial $Z = 0.41$, $P > 0.05$; 0 Hours $Z = 1.38$, $P > 0.05$; 24 Hour $Z = 1.07$, $P > 0.05$; Reversed $Z = 0.97$, $P > 0.05$). Between the pretrial and 0 H periods, females did not exhibit a tendency to remain on the same side of the experimental aviary (binomial test, natural trials: T= 3, $P > 0.05$, $n = 8$, manipulated trials: T = 5, $n = 10$, $P > 0.05$). In the 0 H and 24 H periods, most females remained on the same side (binomial test, natural trials: T = 5, $n = 10$, $P > 0.05$; manipulated trials: T = 8, $n = 10$, $P = 0.01$) indicating that females were likely to associate with the same male in the 0 H and 24 H sampling periods. However, in the 24 H and the reversed sampling periods, females again spent the majority of time on the same side (binomial test, natural trials: T = 7, $n = 9$, $P = 0.02$; manipulated trials: T = 6, $n = 8$, $P = 0.035$), indicating that females did not consistently associate with the same male once the males' positions were reversed.

Morphological variables.—In the trials using natural plumage coloration, males with the

higher color score did not have a longer tarsus length, crest length, tail length, or black bib size (Table 1; Wilcoxon rank tests: all $P > 0.05$). Likewise, males in the reddened and lightened groups did not differ significantly in morphological measurements (Table 2, Wilcoxon rank tests, all $P > 0.05$).

DISCUSSION

During the majority of observation periods, females spent significantly more time with one male. However, the two experiments provided no evidence to support the hypothesis that female Northern Cardinals prefer males with redder or brighter coloration. In trials using natural plumage coloration, females were as likely to spend more time with males having low color scores as with those having high color scores (Fig. 1). Similarly in the manipulated trials, where average plumage differences between males were greater than in the natural trials, females still did not spend more time with redder or brighter males (Fig. 2).

These results differ from other studies of female preference in passerines. Under aviary conditions analogous to the conditions I used, females of many species showed a preference for brightly colored males (Johnson 1988, Hill 1990, Enstrom 1993, Johnson et al. 1993, Sætre et al. 1994, Sundberg 1995; but see Rohwer and Røskaft 1989, Alatalo et al. 1990, Butcher 1991). Although bright plumage colors do not seem important in gallinaceous species, females show preferences for other male ornaments (Zuk et al. 1992, Buchholz 1995, Ligon and Zwartjes 1995, Mateos and Carranza 1995).

The individuals adapted well to captivity and appeared to be in breeding condition. The experiments were conducted at a seasonally appropriate time when pair formation occurs in central New York (pers. obs.). Behaviors associated with pair formation such as singing and slow flight displays occurred in the housing aviaries and during experimental trials, suggesting that males were responding to female presence.

Assigning female preference based on the total time spent with males has become a standard method in avian studies of female choice (Burley et al. 1982, Burley 1986, Hill 1990, Enstrom 1993, Johnson et al. 1993, Sundberg 1995). Observations of pair formation in the field indicate that male and female cardinals interact extensively, consequently time spent with males should be a reasonable indication of mate preference (Kinser 1973).

While males in this study appeared to exhibit some behaviors associated with pair formation, female behavior was more ambiguous. Females flew toward the male area regardless of whether the male was present or not. The side of the aviary on which females spent more time changed from the pretrial to 0 hour sampling period, indicating that females did not immediately establish a preference for one side of the experimental aviary and may have responded to the addition of the males. However, females preferred the same side of the aviary during the 24 hour and reversed sampling periods, even though the males had switched sides. This suggests that after 24 hours individual males did not strongly influence where females spent more time.

With the sample sizes used, the power of the binomial test is high at the critical value. It is noteworthy that other choice experiments of this design have found significant female preferences with similar samples sizes (ranging from 7 to 21 females; Hill 1990, Enstrom 1993, Sætre et al. 1994, Sundberg 1995). This suggests that if a preference for red color exists, it is weak in comparison to color preferences found in other passerines.

The dietary basis of red coloration in male cardinals suggests that females could acquire information about a male's foraging abilities or ability to defend resources using coloration. Male color and his absolute effort in feeding nestlings are not related in cardinals (Linville et al. 1998), emphasizing the limitation of using red coloration alone to assess mates. However, females mated to brighter males fed nestlings less (Linville et al. 1998), suggesting that there may be advantages to pairing with brighter males.

My results provided no evidence for female preference for brighter or redder male plumage coloration as a single criterion for mate choice; however, the possibility remains that female cardinals assess mates using a combination of factors, including coloration, as has been found in other species (Zuk et al. 1990; Omland 1996a, b; Scheffer et al. 1996; Møller et al. 1998). The prolonged opportunities for direct interactions between males and females

prior to pairing (Kinser 1973) suggests that females may be able to use other male characteristics in mate choice, such as song or courtship behaviors. If females assess male condition, multiple ornaments or traits may provide more accurate information either through redundancy or because some ornaments are unreliable indicators of condition (Møller and Pomiankowski 1993). It also remains possible that females assess male coloration in some circumstances but not other. For example, females may use different criteria when choosing social mates and when choosing extra-pair mates.

Lastly, territorial resources may influence mate choices, but coloration may be relatively more important in mediating competition between males. Redder male cardinals acquire territories with denser vegetation density, and pairs on these territories produce more offspring, most likely because of reduced nest predation (Wolfenbarger in press). Given the importance of territory quality, females may directly assess a male's territory during pair formation rather than relying on plumage coloration alone for mate choices.

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FRUIT SUGAR PREFERENCES OF HOUSE FINCHES

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ABSTRACT.—In a series of choice tests, we determined the relative preferences of House Finches (*Carpodacus mexicanus*) for equicaloric aqueous solutions of hexoses (1:1 mixture of fructose and glucose) and sucrose. At 2% (m/v), birds consumed each sugar solution equally and in amounts similar to plain water. Consumption of hexose but not sucrose increased at 4% sugar concentration. At 6% and 10%, finches displayed consistent, strong preferences for the hexoses over sucrose. In other passerine species, strong hexose preference has been linked to the absence of sucrase, the enzyme needed for digestion of sucrose. Fecal sugar readings from the House Finches, however, indicated approximately equal assimilation of hexose and sucrose, so the hexose preference apparently is not due to sucrase deficiency. Rather, energetics may determine the finches' sugar preferences: hexoses are rapidly processed because the 6-carbon sugars are readily assimilable whereas sucrose must first be hydrolyzed. *Received 22 Jan. 1998, accepted 30 Aug. 1998.*

Physiology imposes major constraints on the digestion of sugars by some fruit-eating birds. These constraints in turn affect species' food selection behavior. Species of Sturnidae (e.g., European Starling, *Sturnus vulgaris*) and Turdidae (e.g., American Robin, *Turdus migratorius*) are unable to digest sucrose because they lack the enzyme sucrase needed to hydrolyze sucrose into 6-carbon sugars, glucose and fructose that can be assimilated (Martínez del Rio and Stevens 1989, Karasov and Levey 1990). Ingestion of high concentrations of sucrose by these species produces osmotic diarrhea and, in extreme cases, death (Martínez del Rio et al. 1988, Brugger and Nelms 1991). Consequently, in feeding and drinking trials starlings and robins learn to avoid sucrose (Schuler 1983, Martínez del Rio et al. 1988, Brugger 1992).

Although Cedar Waxwings (*Bombycilla cedrorum*) can digest sucrose, in choice tests they also prefer hexoses to sucrose (Martínez del Rio et al. 1989, Avery et al. 1995). Waxwings exhibit very rapid gut passage rates (Levey and Grajal 1991). As a result, sucrose is not in the gut long enough to be completely hydrolyzed and is therefore inefficiently assimilated relative to hexose sugars (Martínez del Rio et al. 1989).

In the Icteridae and Emberizidae, two frugivorous species, the Yellow-winged Cacique (*Cacicus melanicterus*) and the Yellow-breasted Chat (*Icteria virens*) preferred 15% (by mass) hexose solution over sucrose solution and displayed relatively inefficient sucrose digestion (Martínez del Rio and Restrepo 1993). Conversely, Red-winged Blackbirds (*Agelaius phoeniceus*) and Common Grackles (*Quiscalus quiscula*), granivorous icterids, preferred sucrose solutions to water but did not distinguish between 0.175M and 0.35M hexose solutions and water (Martínez del Rio et al. 1988).

The House Finch (*Carpodacus mexicanus*) is primarily granivorous (Martin et al. 1951) but feeds opportunistically on cultivated fruit (Tobin and DeHaven 1984, Avery et al. 1992). To our knowledge the sugar preferences of House Finches and other Fringillidae have not been evaluated. Responses of House Finches to fruit sugars are pertinent to the development of high-sucrose fruit cultivars for potentially reducing bird damage to fruit crops (Brugger et al. 1993, Darnell et al. 1994). Thus, our objectives were (1) to document House Finch consumption of sucrose and hexose in equicaloric aqueous solutions across a range of sugar concentrations typically found in cultivated fruit and (2) to measure fecal sugar to determine relative digestion of sucrose and hexoses.

METHODS

House Finches were from a captive population maintained at the Florida Field Station of the U.S. Dept. of Agriculture's National Wildlife Research Center in Gainesville, Florida. We maintained birds on a mixed seed diet supplemented three days/week with

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apples and lettuce. Testing occurred during October–November 1995. After testing, birds were returned to their home cages.

We removed birds from communal enclosures (2 × 1.5 × 2.2 m) and placed them into individual, visually isolated test cages (45 cm on a side) in a roofed outdoor aviary. To acclimate the birds, we offered plain water tinted with red food coloring in clear glass tubes (8 mm diameter) 4–5 days before testing. We fixed two tubes, 5 cm apart, to the front of each cage. During acclimation, we measured water consumption after 6 h and 24 h daily to determine baseline fluid intake and to accustom the birds to disturbances.

We prepared test solutions by dissolving 20, 40, 60, or 100 g of sucrose or hexose sugars (Sigma Chemical Company, St. Louis, Missouri) in 1 L of distilled water. The hexose solution contained equal amounts of fructose and glucose. We then conducted separate tests at each of 4 sugar concentrations (m/v): 2%, 4%, 6%, and 10%. Tests lasted 4 days and there were 6 birds/group. One hexose tube and one sucrose tube, 5 cm apart, were available during each test. For each cage, we first randomly determined the position of the sucrose tube and then alternated sucrose and hexose positions daily. We removed maintenance food and water at 08:00 and presented the tubes with sugar solutions from 09:00 until 15:00. Maintenance food and water were then returned to the cages.

We measured the amount of solution missing from each tube to the nearest mm, and then converted to amount of sugar (g) ingested for analyses. We assessed sugar consumption in a 3-way analysis of variance, with sugar concentration as the independent factor, and repeated measures over sugar type and days. We used Tukey's HSD test (Steel and Torrie 1980) to isolate differences ($P < 0.05$) among means.

To determine relative digestion by finches of sucrose and hexoses, we analysed fecal sugar with a hand-held refractometer (Hainesworth 1974, Brugger et al. 1993). We offered six birds a 10% (m/v) agar-sucrose mixture (Avery et al. 1995) for 6 hours and offered similar food made with hexose (equal amounts of glucose and fructose) for 6 hours the next day. We measured three fresh defecations from each bird with each sugar treatment, and compared mean values in a paired *t*-test against a null hypothesis of no difference between sugars. Refractometer readings are expressed as degrees Brix which corresponds to the percentage of sugar present in the sample on a mass:mass basis (Bolten et al. 1979).

RESULTS

Total sugar consumption varied ($F_{1,20} = 22.77$, $P < 0.001$) with concentration. Sugar ingestion at 6% (mean ± SE, $\bar{x} = 1.07 \pm 0.12$ g/bird) and 10% ($\bar{x} = 1.66 \pm 0.11$ g/bird) exceeded that at 2% ($\bar{x} = 0.03 \pm 0.01$ g/bird) and 4% ($\bar{x} = 0.29 \pm 0.08$ g/bird). Overall, hexose consumption (0.67 ± 0.07 g/bird) exceeded ($F_{1,20} = 93.55$, $P < 0.001$) sucrose

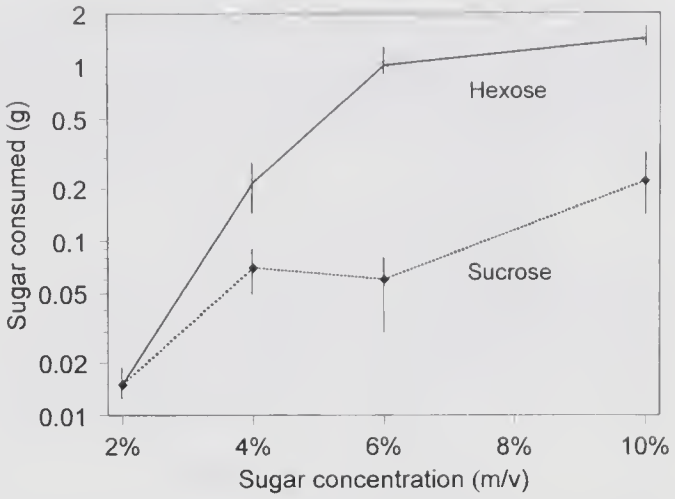

FIG. 1. Mean consumption of hexoses and sucrose by House Finch groups (6 birds/group) exposed to two tubes of aqueous sugar solutions for 4 days, 6 hours per day. Vertical bars denote 1 SE. Note that the y axis is logarithmic.

consumption (0.09 ± 0.02 g/bird). Finches consumed less sugar ($F_{3,60} = 2.83$, $P = 0.046$) on day 1 (0.61 ± 0.17 g/bird) than on days 2–4 (mean consumption 0.79–0.83 g/bird).

Across the range of test concentrations, finches responded differently ($F_{3,20} = 24.78$, $P < 0.001$) to the two types of sugars (Fig. 1). Sucrose consumption was consistently low (mean consumption 0.02–0.22 g/bird) and did not differ from hexose consumption at 2% (0.02 ± 0.01 g/bird) and 4% (0.22 ± 0.07 g/bird). Hexose consumption increased ($P < 0.05$) substantially, however, at 6% (1.01 ± 0.11 g/bird) and at 10% (1.43 ± 0.10 g/bird).

The interaction between type of sugar and test day affected consumption ($F_{3,60} = 16.59$, $P < 0.001$). Sucrose consumption did not differ across the 4 test days, and on day 1, mean sucrose consumption (0.22 ± 0.10 g/bird) equalled hexose consumption (0.39 ± 0.10 g/bird). Hexose consumption increased thereafter and averaged 0.73 to 0.79 g/bird on days 2–4.

The 3-way interaction ($F_{9,60} = 5.31$, $P < 0.001$) reflected differing daily consumption patterns of the two sugar types as sugar concentration varied (Fig. 2). At 2%, consumption of both types of sugar remained low throughout the test. At 4%, mean hexose consumption increased each day but not sufficiently to achieve statistical significance ($P > 0.05$). At 6%, mean hexose consumption increased ($P < 0.05$) from day 1 (0.66 ± 0.21

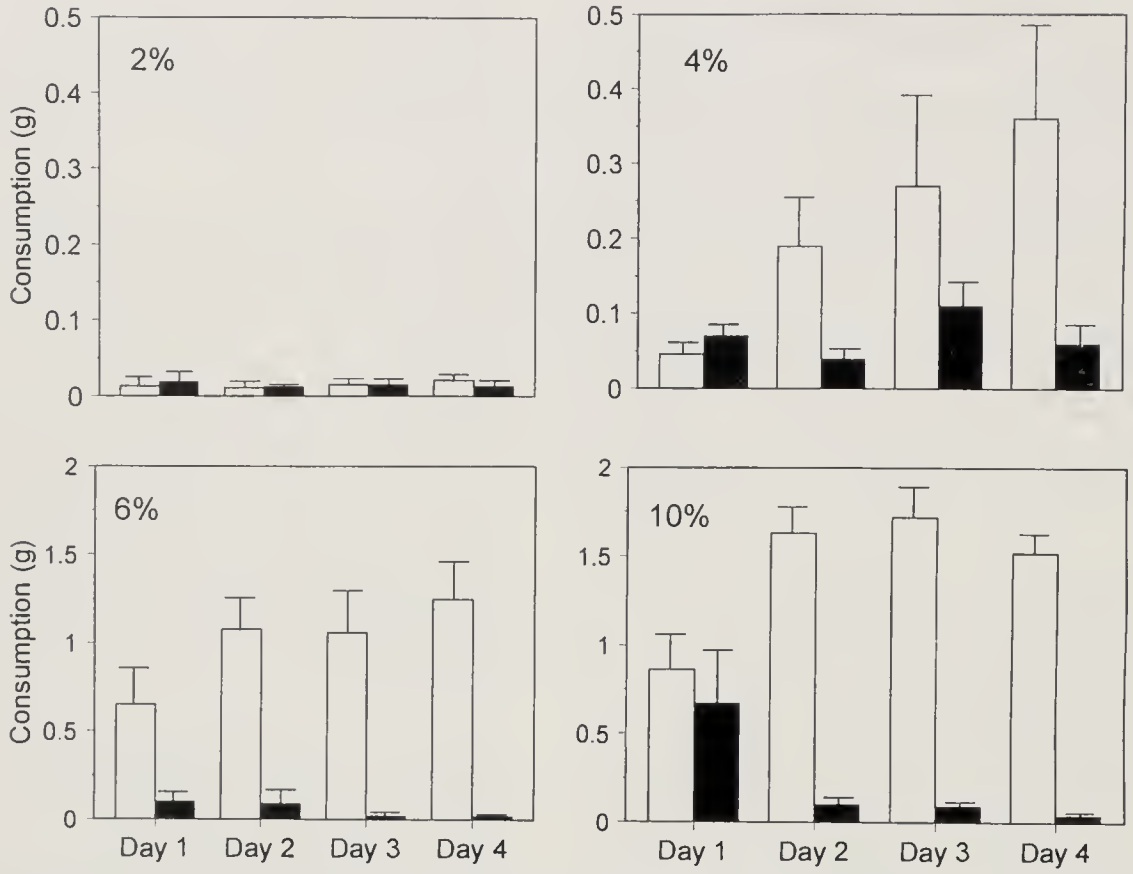

FIG. 2. Mean daily consumption of hexoses (open bars) and sucrose (solid bars) by House Finches (6 birds/trial) exposed to two tubes of aqueous sugar solutions for 6 hours each day. Vertical bars denote 1 SE.

g/bird) to day 4 (1.25 ± 0.22 g/bird). On day 1, finches consumed equal amounts of hexose and sucrose at the 10% level, but consumption diverged ($P < 0.05$) on day 2 and remained so through day 4.

During pretest days, hourly consumption of water averaged 0.22 ± 0.10 and 0.33 ± 0.07 ml/bird for the 2% and 4% groups, respectively, similar to their total consumption of 2% (0.25 ± 0.03 ml/bird) and 4% (1.19 ± 0.30 ml/bird) sugar solutions. Fecal sugar analysis from six birds revealed no difference ($t = 1.63$, $P > 0.05$) between sugars. Hexose readings averaged 4.2 ± 0.7° Brix compared to an average of 2.8 ± 0.3° Brix for sucrose.

DISCUSSION

In the range of concentrations we tested, preference for hexose over sucrose has not previously been demonstrated, even in species lacking sucrase. Rejection of sucrose by European Starlings and American Robins occurred at concentrations in excess of 10% (Schuler 1983, Martínez del Rio et al. 1988, Brugger 1992). Other species are either indifferent (domestic hen, Kare and Medway 1959; Rock Dove, *Columba livia,* Duncan 1960; Common Raven, *Corvus corax,* Harriman and Fry 1990) or prefer sucrose (Common Grackle, Red-winged Blackbird; Martínez del Rio et al. 1988). In choice tests, hummingbirds prefer sucrose and reject fructose (Stiles 1976), but when fructose is offered alone, hummingbirds consume it at a rate no different from sucrose. Other nectarivorous species also select sucrose preferentially over equimolar fructose and glucose solutions (Downs and Perrin 1996).

The sugar solutions we offered appeared alike to us and their relative positions were switched daily. At 2%, it appeared that finches did not distinguish dilute sugar solutions from plain water; consumption was low and remained so throughout the trial. Finches responded to sugar at the 4% level, and mean consumption of hexose increased steadily across the 4-day trial while sucrose consumption remained low. At 6%, hexose consumption increased markedly over that at 2% and 4%, while sucrose consumption did not differ from that at lower concentrations. Discrimination between sugars was more rapid at 10%,

as finches decisively selected hexose over sucrose after one trial. The birds apparently tracked the position of the hexose tube through a nonvisual cue. The mechanism by which they discriminated hexose from sucrose is unclear, but the rapidity of the discrimination increased with sugar concentration.

We hypothesize that finches chose hexoses in response to an increased rate of energy gain relative to sucrose solutions during the 6-h drinking trials. Birds are sensitive to differences in rates of energy assimilation (Witmer 1994), and the extra step, hydrolysis of the sucrose molecule required for sucrose digestion imposes a constraint on the potential rate of energy assimilation. In our choice tests, finches responded facultatively and selected the more energetically efficient food source.

Martínez del Rio and coworkers (1988) predicted that granivores should have high sucrase activity and prefer, or at least tolerate, sucrose. This follows from the facts that maltose is the major constituent of complex carbohydrates found in seeds, granivorous species show high intestinal maltase activity, and the activity of sucrase seems to vary with that of maltase and isomaltase (Martínez del Rio 1990, Martínez del Rio et al. 1995). Although House Finches are basically granivorous, they strongly favored moderate hexose sugar solutions over sucrose (Figs. 1, 2). We did not determine intestinal enzyme activity directly, but fecal sugar analyses indicated that the preference for hexoses was not because of absence of sucrase. House Finches prefer hexose sugars but are "sucrose tolerant" granivores, consistent with the hypothesis of Martínez del Rio and coworkers (1988). Comparative studies of House Finches and other granivores will help to define more clearly the physiological basis underlying their food selection behavior.

Development of high-sucrose fruit cultivars could represent one nonlethal component of an integrated plan to manage bird damage to berry crops (Brugger et al. 1993, Darnell et al. 1994). Such an approach will most likely be effective against species such as the European Starling and American Robin that lack sucrase and are thus unable to digest sucrose. For sucrose tolerant species such as the House Finch, elevated sucrose concentrations in fruit will probably not reduce crop damage unless alternative food sources are readily available. Rather, because of inefficient energy assimilation from sucrose ingestion, sucrose tolerant species might compensate by increasing fruit consumption, thereby causing greater damage (Avery et al. 1995).

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HIERARCHICAL COMPARISONS OF BREEDING BIRDS IN OLD-GROWTH CONIFER-HARDWOOD FOREST ON THE APPALACHIAN PLATEAU

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ABSTRACT.—I compared relative abundances of breeding birds in old-growth forest (≥300 years old) to surrounding landscapes using data from the Breeding Bird Census (BBC) and Breeding Bird Atlas (BBA). Eleven study plots (148 ha total) were established in relict, presettlement hemlock-white pine-northern hardwood (*Tsuga canadensis-Pinus strobus*) forest on the northern Appalachian Plateau, Pennsylvania. Of 56 breeding species recorded in old-growth forest, 34% were either uncommon (≤25% of BBA blocks) or rare (≤10% of BBA blocks) in adjacent landscape units. A species accumulation curve indicated that about 40 species recurred in old-growth habitat. This avian community included species less likely to occur in oldgrowth, forest interior species showing a statistically neutral relationship to oldgrowth, and habitat specialists more likely to reside in oldgrowth than in the landscape at large. The last group included several taxa linked to structural features of oldgrowth elsewhere in North America: Hairy Woodpecker (*Picoides villosus*), Red-breasted Nuthatch (*Sitta canadensis*), Brown Creeper (*Certhia americana*), Winter Wren (*Troglodytes troglodytes*), Golden-crowned Kinglet (*Regulus satrapa*), *Empidonax* flycatchers, and several species of arboreal *Dendroica* warblers. *Received 14 July 1998, accepted 4 Nov. 1998.*

Old-growth forests possess unique ecological characteristics that can exert profound influence on some bird populations and communities (Hunter et al. 1995, Dellasala et al. 1996). Ecological importance of oldgrowth to birds is poorly known in much of North America, largely because late successional forest outside the Pacific Northwest now occurs only in relict patches (Davis 1996). Ideally, the role of old-growth forest in facilitating avian diversity could be best evaluated by comparing species occurrences within entire landscapes made up of many different habitats.

What is the best way to evaluate bird distributions and abundances over multiple spatial scales? Results of studies on species occurrences at any one scale may conflict with results at alternative scales (Conroy and Noon 1996). In avian ecology, this concern may find expression as a tradeoff among within-habitat (α), between-habitat (β), and landscape (γ) diversity (Whittaker 1977, Wiens 1989). For avian conservation, management actions at local scales must be weighed against their consequences at broader scales in order to optimize benefits of land use (Flather 1996). A hierarchical framework is the method usually recommended to address such scale dependency (Kotliar and Wiens 1990).

I used a landscape hierarchy to evaluate bird distribution and abundance in old-growth forest, once a widespread vegetation type in eastern North America. Local species' occurrences in old-growth conifer-hardwood forest were compared to occurrences in the surrounding landscape using data from the Breeding Bird Census and Breeding Bird Atlas. Three questions were posed: (1) can a metric be devised to compare bird species occurrences across different spatial scales, (2) does old-growth forest harbor birds determined independently to be uncommon or rare in larger landscape units, and (3) which individual species are more likely to occur in old-growth than in the landscape as a whole?

METHODS

Study area.—Bird communities in oldgrowth were studied within three permanent forest reserves in Pennsylvania: Cook Forest State Park, Heart's Content, and Tionesta Scenic and Research natural areas in the Allegheny National Forest (41° 20′–41° 42′ N, 78° 56′–79° 15′ W). Tract sizes of old-growth habitat varied from 1000 ha at Tionesta to 60 ha at Heart's Content; each of these reserves is embedded within much larger contiguous tracts of younger managed forest. Landscape fragmentation is greater in Cook Forest where developed and agricultural lands virtually surround this 3000 ha reserve (which includes some 200 ha of old-growth in three sites). All reserves are located on the northern Appalachian Plateau (212Ga: Allegheny High

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Plateau Subsection, Northern Unglaciated Allegheny Plateau Section; Keys et al. 1995), a region characterized by broad, flattened ridges (500–700 m) and dissected by deep, V-shaped valleys. Higher precipitation and greater cloud cover create a cooler, more humid climate compared to adjacent regions (Whitney 1990).

Each reserve possesses relict stands of true old-growth, stands with extreme ecological maturity (Leverett 1996). The forest consists of hemlock-white pine-northern hardwoods (Nichols 1935), a cover type that most closely resembles USDA Forest Service CISC (continuous inventory of stand condition) types 4 and 8, Society of American Foresters forest type code 22 (Eyre 1980), and International Classification of Ecological Communities I.B.8.N.b.150 (USDA 1997). Canopy dominants include eastern hemlock (*Tsuga canadensis*), eastern white pine (*Pinus strobus*), yellow birch (*Betula alleghaniensis*), black birch (*Betula lenta*), sugar maple (*Acer saccharum*), red maple (*Acer rubrum*), and American beech (*Fagus grandifolia*; Whitney 1990).

Understories are generally sparse with little herbaceous ground cover. Canopy trees at each site are 300–530 years old (Hough and Forbes 1943; Abrams and Orwig 1996; Stahle 1996; C. Nowack, pers. comm.), and so are beyond the threshold (275 years) at which unique structure begins to develop in this community type (Tyrrell and Crow 1994). Typical of forest in presettlement condition, most stands have ecological attributes that are rare or absent in younger, managed forests (e.g., 57 metric tons of coarse woody debris ha^{-1}; >⅓ of stand basal area in trees >70 cm diameter at breast height; Haney, unpubl. data).

Since the late 1800s conifer-hardwood forest in the eastern U.S. has been fragmented into isolated blocks, markedly reduced in area, and converted into cover types dominated by younger, shade intolerant hardwoods. On the northern Appalachian Plateau, the old-growth hemlock-hardwood forest once covered 2.4 million ha (Bjorkblom and Larson 1977), but today it is reduced to no more than 20% of its presettlement extent (Whitney 1990, Abrams and Ruffner 1995).

Data collection.—I used the Breeding Bird Census (BBC; Hall 1964) to evaluate bird species occurrences within old-growth habitat. Breeding Bird Census methodology is used primarily to assess local population density by counting the number of breeding territories on a few ha. Five BBC plots (15–18 ha each) were located in Cook Forest, two (10–12 ha) in Heart's Content, and four (12 ha) in Tionesta. Individual plots within sites at each reserve ranged from 200 m to 2500 m apart. Breeding birds were counted during eight or more visits to each plot during May and June 1994 using standard protocols (Hall 1964, Lowe 1993). Each plot was visited on a different day, usually within a few minutes of sunrise. Two visits were made at dusk. Each visit lasted about two hours, which resulted in a census speed of about 9 min ha^{-1} and is comparable to speeds deemed appropriate for relatively open forests (Engstrom and James 1984).

On each visit, an observer walked slowly along a flagged census line through the plot, delineating all bird territories on grid maps. Birds were detected both visually and acoustically, but most detections were acoustic. The census line was configured to place the observer no more than 50 m from any part of the plot so as to reduce detection bias from acoustic attenuation (Schieck 1997). Numbers of territories were then calculated from grid maps using standard spot-mapping procedures (Hall 1964).

The Pennsylvania Breeding Bird Atlas project (1983–1989) was a grid-based survey using techniques developed originally in Britain and Ireland, with standards modified for the northeastern U.S. (Laughlin 1982). Atlas projects are used primarily for broad mapping of avian distributions and rely upon a network of volunteer field ornithologists to document breeding evidence at three levels of certainty ("possible," "probable," and "confirmed"). In Pennsylvania, the basic sampling units consisted of 7.5′ U.S. Geological Survey topographic maps divided into six equal-size blocks formed longitudinally by 3.75′ intervals and latitudinally by 2.5′ intervals (Brauning 1992). Atlas efforts were undertaken in both summer and winter within known "safe" dates for nesting activity of all species. Based on previous theoretical and empirical work, blocks were considered adequately covered if 75–80% of the expected species were found, 10–20 hours of survey effort were expended, or 70 or more species were recorded.

Community level analyses.—To test whether sampling effort was adequate for characterizing the total species complement (S_{max}) of the old-growth bird community, I conducted two analyses on the area curve of cumulative species richness (S). The shape of species accumulation curves depends on the order in which samples are added, a feature not modeled well with parametric methods (Bunge and Fitzpatrick 1993). I used non-parametric routines to randomize sample order (PISCES 1.2 software, Windows 95 version; Henderson and Seahy 1997). For greater resolution in constructing the species accumulation curve, I first subsampled the BBC data at a scale of 3 ha. From each and all of the 11 original study plots, I randomly selected and ordered 3 ha subplots and scored bird species occurrences and territorial densities using methods identical to those used in the original large plots.

Accurate estimation of S_{max} is possible only if the species accumulation curve is derived from a homogenous community (Henderson and Seahy 1997). I first compared the mean randomized curve (1000 iterations) with a curve expected if all individual birds recorded over all the samples were assigned randomly to individual samples (Colwell and Coddington 1994). If the expected curve (Coleman et al. 1982) rises more sharply from its origin, then heterogeneity is greater than can be explained by chance. Such a result could indicate that the samples were a combination of distinct bird communities or derived from different habitats (Flather 1996).

Asymptotic models of species accumulation curves are usually appropriate for homogenous communities

(Henderson and Scahy 1997). I calculated S_{max} using a non-parametric maximum likelihood estimater (Raaijmakers 1987) in which sampling is assumed to be complete when the asymptotic estimate is equal to or less than the observed. This procedure was applied incrementally to larger combinations of randomly shuffled 3 ha subplots (1000 iterations each) until the "stopping rule" indicated that sampling of the old-growth bird community was sufficient.

Species level analyses.—I used incidence (frequency in a set of samples; Wright 1991) as the metric to compare individual species' occurrences in oldgrowth to their occurrence in landscape units. Incidence in old-growth samples was calculated by dividing the number of plots containing each species by 11. For Pennsylvania and the northern Appalachian Plateau, I used the proportion of BBA blocks recording that species for each of the two landscape divisions. The atlas program covered a total of 4928 and 2027 BBA blocks state and province wide, respectively (Brauning 1992). Species recorded in less than 25% and 10% of BBA blocks in either landscape division were considered uncommon and rare, respectively.

I compared incidence in oldgrowth (I_{OG}) to incidence statewide (I_{ST}) and province-wide (I_{AP}) with the normal deviate, Z, where:

$$Z = (I_1 - I_2)/(I \times (1 - I)(1/N_1 + 1/N_2))^{0.5},$$

and I and $1 - I$ are the joint probabilities of the combined incidences in the two sample proportions of finding and not finding that species, respectively (Snedecor and Cochran 1980). I used Pearson's product moment correlation to test whether incidence was related to the natural log of population density (number of breeding territories). Log transformations on population density were used to smooth variances in data composed of whole integers (Snedecor and Cochran 1980). Values of test statistics were considered significant at $P \leq 0.05$ unless otherwise indicated.

RESULTS

Community composition.—Fifty-six species were recorded in 148 ha of old-growth forest across the 11 study plots (Table 1). Thirteen species were found in only one plot (incidence value = 0.091). Another species, Downy Woodpecker (*Picoides pubescens*), was recorded in two plots, but less than one full territory was recorded in each plot. Without considering these 14 species, a recurring complement of 42 species was identified in which full breeding territories were established in two or more of the 11 study plots (Table 2).

The observed species accumulation curve (Fig. 1) did not differ from the curve expected in a homogenous community ($\chi^2 = 0.25$, $P > 0.05$, df = 27). Thus, this analysis gave no indication that more than one bird community was being sampled. The estimated asymptotic value (38.6) for species richness fell below the observed value (39) after 1000 randomizations of 28 3-ha subplots. This level of effort corresponded to 84 ha (57%) of the total area actually sampled in this study.

Species groups.—About one-third of all species recorded as breeders in old-growth conifer-hardwood were either uncommon or rare over broad spatial scales (Table 1). Nineteen species (34%) were more likely to occur in oldgrowth than in the landscape unit consisting of the entire state. Sixteen species (29%) were more likely to occur in oldgrowth than in the landscape unit of the northern Appalachian Plateau. Fifteen individual species were more likely to occur in oldgrowth than in the landscape at both state and province levels (Table 2). Red-shouldered Hawk (*Buteo lineatus*) and Barred Owl (*Strix varia*) were more likely to occur in oldgrowth than in the landscape unit consisting of the entire state but not the northern Appalachian Plateau.

Seventeen species were less likely to occur in old-growth forest than in the landscape at large (Table 2). This group included permanent resident, habitat generalists [e.g., American Crow (*Corvus brachyrhynchos*)] as well as some Neotropical migrants with more specific habitat preferences [e.g., cavity-nesting Great Crested Flycatcher (*Myiarchus crinitus*)].

No species showing negative association with oldgrowth (Table 2) was rare at the state level, and none of the species in this group was either rare or uncommon at the level of the physiographic province (Table 1). Only one species, Black-throated Blue Warbler (*Dendroica caerulescens*), was uncommon at the state level (15% of BBA blocks). Most species negatively associated with oldgrowth were very widespread within broad landscape units, occurring in 50–90% of the BBA blocks.

Based on statistical criteria, 10 species were neither more nor less likely to occur in old-growth than in at least one of the larger landscape units (Tables 1 and 2). All species in this group rely upon forest interior habitat, including the raptors Red-shouldered Hawk and Barred Owl, and Neotropical migrant songbirds such as Red-eyed Vireo (*Vireo oliva-*

TABLE 1. Relative occurrence of breeding birds in old-growth hemlock-white pine-hardwood forest on the northern Appalachian Plateau, Pennsylvania. Incidence (I) of each species in oldgrowth (proportion of study plots, $n = 11$) is compared to incidence across the entire state and within the physiographic province [proportion of Breeding Birds Atlas (BBA) plots recording the species; $n = 4928$ and 2027 blocks, respectively].

Species	Incidence			Comparison			
				$(I_{OG}) - (I_{ST})$		$(I_{OG}) - (I_{AP})$	
	Oldgrowth (I_{OG})	Statewide (I_{ST})	Appalachian Plateau (I_{AP})	Z^a	P	Z^a	P
Common Merganser (*Mergus merganser*)	0.091	0.046	0.087	0.71	>0.05	0.56	>0.05
Sharp-shinned Hawk (*Accipiter striatus*)	0.091	0.213	0.200	−0.99	>0.05	−0.90	>0.05
Red-shouldered Hawk (*Buteo lineatus*)	0.364	0.152	0.223	1.95	0.026	1.12	>0.05
Mourning Dove (*Zenaida macroura*)	0.273	0.917	0.835	−7.68	<0.001	−4.97	<0.001
Barred Owl (*Strix varia*)	0.455	0.218	0.277	1.90	0.029	1.31	>0.05
Ruby-throated Hummingbird (*Archilochus colubris*)	0.273	0.714	0.704	−3.23	0.001	−3.12	0.001
Yellow-bellied Sapsucker (*Sphyrapicus varius*)	0.273	0.149	0.319	1.15	>0.05	−0.33	>0.05
Downy Woodpecker (*Picoides pubescens*)	0.182	0.890	0.855	−7.45	<0.001	−6.26	<0.001
Hairy Woodpecker (*Picoides villosus*)	0.909	0.632	0.643	1.90	0.029	1.84	0.033
Northern Flicker (*Colaptes auratus*)	0.091	0.917	0.873	−9.82	<0.001	−7.66	<0.001
Pileated Woodpecker (*Dryocopus pileatus*)	0.545	0.538	0.566	0.05	>0.05	−0.14	>0.05
Eastern Wood-Pewee (*Contopus virens*)	0.091	0.883	0.868	−8.11	<0.001	−7.49	<0.001
Yellow-bellied Flycatcher (*Empidonax flaviventris*)	0.091	0.003	0.006	5.16	<0.001	3.51	<0.001
Acadian Flycatcher (*Empidonax virescens*)	0.818	0.358	0.234	3.18	0.001	4.54	<0.001
Least Flycatcher (*Empidonax minimus*)	0.182	0.369	0.636	−1.29	>0.05	−3.12	0.001
Greater Crested Flycatcher (*Myiarchus crinitus*)	0.182	0.709	0.640	−3.84	<0.001	−3.15	0.001
Blue Jay (*Cyanocitta cristata*)	0.636	0.954	0.939	−4.99	<0.001	−4.13	<0.001
American Crow (*Corvus brachyrhynchos*)	0.182	0.978	0.964	−17.31	<0.001	−13.17	<0.001
Common Raven (*Corvus corax*)	0.182	0.172	0.294	0.09	>0.05	−0.81	>0.05
Tufted Titmouse (*Baeolophus bicolor*)	0.273	0.809	0.641	−4.51	<0.001	−2.54	0.006
Black-capped Chickadee (*Poecile atricapillus*)	1.000	0.842	0.970	1.44	>0.05	0.58	>0.05
Red-breasted Nuthatch (*Sitta canadensis*)	0.727	0.041	0.064	11.27	<0.001	8.74	<0.001
White-breasted Nuthatch (*Sitta carolinensis*)	0.545	0.828	0.840	−2.48	0.006	−2.65	0.004
Brown Creeper (*Certhia americana*)	1.000	0.231	0.324	6.03	<0.001	4.76	<0.001
Winter Wren (*Troglodytes troglodytes*)	0.909	0.077	0.147	10.23	<0.001	7.04	<0.001
Golden-crowned Kinglet (*Regulus satrapa*)	0.182	0.037	0.057	2.53	0.006	1.77	0.038
Swainson's Thrush (*Catharus ustulatus*)	0.636	0.009	0.019	20.49	<0.001	13.82	<0.001
Hermit Thrush (*Catharus guttatus*)	1.000	0.278	0.492	5.33	<0.001	3.36	<0.001
Wood Thrush (*Hylocichla mustelina*)	0.182	0.912	0.892	−8.47	<0.001	−7.45	<0.001
American Robin (*Turdus migratorius*)	0.364	0.991	0.987	−20.49	<0.001	−16.25	<0.001
Cedar Waxwing (*Bombycilla cedrorum*)	0.182	0.824	0.919	−5.57	<0.001	−8.74	<0.001
Blue-headed Vireo (*Vireo solitarius*)	1.000	0.299	0.484	5.07	<0.001	3.41	<0.001

TABLE 1. CONTINUED

Species	Incidence			Comparison			
				$(I_{OG}) - (I_{ST})$		$(I_{OG}) - (I_{AP})$	
	Oldgrowth (I_{OG})	Statewide (I_{ST})	Appalachian Plateau (I_{AP})	Z[a]	P	Z[a]	P
Red-eyed Vireo (*Vireo olivaceus*)	1.000	0.931	0.959	0.90	>0.05	0.69	>0.05
Northern Parula (*Parula americana*)	0.091	0.101	0.099	−0.11	>0.05	−0.09	>0.05
Chestnut-sided Warbler (*Dendroica pensylvanica*)	0.091	0.407	0.686	−2.13	0.017	−4.23	<0.001
Magnolia Warbler (*Dendroica magnolia*)	1.000	0.151	0.315	7.82	<0.001	4.86	<0.001
Black-throated Blue Warbler (*Dendroica caerulescens*)	0.455	0.150	0.272	2.82	0.002	1.36	>0.05
Yellow-rumped Warbler (*Dendroica coronata*)	0.091	0.064	0.126	0.36	>0.05	−0.35	>0.05
Black-throated Green Warbler (*Dendroica virens*)	1.000	0.366	0.587	4.36	<0.001	2.78	0.003
Blackburnian Warbler (*Dendroica fusca*)	1.000	0.186	0.350	6.90	<0.001	4.50	<0.001
Bay-breasted Warbler (*Dendroica castanea*)[b]	0.091	—	—	—	—	—	—
Pine Warbler (*Dendroica pinus*)	0.364	0.060	0.057	4.21	<0.001	4.32	<0.001
Black-and-white Warbler (*Mniotilta varia*)	0.091	0.428	0.501	−2.26	0.012	−2.71	0.003
American Redstart (*Setophaga ruticilla*)	0.182	0.607	0.796	−2.88	0.002	−5.01	<0.001
Ovenbird (*Seiurus aurocapillus*)	0.364	0.746	0.827	−2.91	0.002	−4.03	<0.001
Mourning Warbler (*Oporornis philadelphia*)	0.091	0.048	0.111	0.66	>0.05	−0.21	>0.05
Common Yellowthroat (*Geothlypis trichas*)	0.182	0.960	0.975	−12.89	<0.001	−15.56	<0.001
Hooded Warbler (*Wilsonia citrina*)	0.364	0.288	0.313	0.55	>0.05	0.36	>0.05
Scarlet Tanager (*Piranga olivacea*)	1.000	0.868	0.903	1.29	>0.05	1.09	>0.05
Rose-breasted Grosbeak (*Pheucticus ludovicianus*)	0.364	0.639	0.835	−1.90	0.029	−4.17	<0.001
Indigo Bunting (*Passerina cyanea*)	0.091	0.946	0.931	−12.33	<0.001	−10.65	<0.001
Chipping Sparrow (*Spizella passerina*)	0.909	0.971	0.976	−1.22	>0.05	−1.44	>0.05
Dark-eyed Junco (*Junco hyemalis*)	1.000	0.271	0.528	5.42	<0.001	3.13	0.001
Brown-headed Cowbird (*Molothrus ater*)	0.364	0.877	0.834	−5.16	<0.001	−4.16	<0.001
Purple Finch (*Carpodacus purpureus*)	0.909	0.294	0.485	4.47	<0.001	2.81	0.003
American Goldfinch (*Carduelis tristis*)	0.091	0.944	0.924	−12.10	<0.001	−10.13	<0.001

[a] Test statistic (normal deviate) on the difference between proportions: positive values of Z indicate a greater incidence of that species in oldgrowth, negative values indicate lower incidence in oldgrowth.

[b] Unrecorded during the state's 5 year BBA project. From 1993–1995, an irruption of the elm spanworm *Ennomus subsignarius* affected much of Pennsylvania's forests. Several birds influenced by geometrid outbreaks were recorded during these breeding seasons for the first time: Bay-breasted Warbler, Blackpoll Warbler (*Dendroica striata*) and Evening Grosbeck (*Coccothraustes vespertinus*).

TABLE 2. Number of territories and population densities (number territories/10 ha) of the core community of breeding birds in all plots (n = 11) of old-growth hemlock-white pine-hardwood forest on the northern Appalachian Plateau, Pennsylvania.

Association: Species[a]	Total territories	Territorial density	
		Mean	SE
Positive old-growth affinity:			
Hairy Woodpecker (*Picoides villosus*)	12.5	0.50	0.42
Acadian Flycatcher (*Empidonax virescens*)	24.5	1.27	1.57
Red-breasted Nuthatch (*Sitta canadensis*)	10	0.40	0.36
Brown Creeper (*Certhia americana*)	31	1.58	0.71
Winter Wren (*Troglodytes troglodytes*)	30.5	1.73	0.98
Golden-crowned Kinglet (*Regulus satrapa*)	4	0.10	0.23
Swainson's Thrush (*Catharus ustulatus*)	35	2.08	2.42
Hermit Thrush (*Catharus guttatus*)	36.5	1.90	1.49
Blue-headed Vireo (*Vireo solitarius*)	88	4.57	2.26
Magnolia Warbler (*Dendroica magnolia*)	185	11.10	2.70
Black-throated Green Warbler (*Dendroica virens*)	176	9.41	5.36
Blackburnian Warbler (*Dendroica fusca*)	410	23.94	8.25
Pine Warbler (*Dendroica pinus*)	5	0.17	0.25
Dark-eyed Junco (*Junco hyemalis*)	83	4.09	0.92
Purple Finch (*Carpodacus purpureus*)	17	0.72	0.52
Neutral oldgrowth affinity:			
Red-shouldered Hawk (*Buteo lineatus*)[b]	2.5	0.09	0.13
Barred Owl (*Strix varia*)[b]	4.5	0.18	0.24
Yellow-bellied Sapsucker (*Sphyrapicus varius*)	4	0.14	0.26
Pileated Woodpecker (*Dryocopus pileatus*)	5.5	0.25	0.31
Common Raven (*Corvus corax*)	1.5	0.07	0.19
Black-capped Chickadee (*Poecile atricapillus*)	24	1.14	0.62
Red-eyed Vireo (*Vireo olivaceus*)	110	5.22	3.06
Hooded Warbler (*Wilsonia citrina*)	15	0.87	1.40
Scarlet Tanager (*Piranga olivacea*)	42.5	2.23	1.08
Chipping Sparrow (*Spizella passerina*)	20	1.00	0.63
Negative old-growth affinity:			
Mourning Dove (*Zenaida macroura*)	3	0.09	0.21
Ruby-throated Hummingbird (*Archilochus colubris*)	2	0.06	0.11
Least Flycatcher (*Empidonax minimus*)	3.5	0.18	0.53
Great Crested Flycatcher (*Myiarchus crinitus*)	1.5	0.08	0.18
Blue Jay (*Cyanocitta cristata*)	10.5	0.45	0.35
American Crow (*Corvus brachyrhynchos*)	1.5	0.06	0.14
Tufted Titmouse (*Baeolophus bicolor*)	2	0.11	0.19
White-breasted Nuthatch (*Sitta carolinensis*)	7.5	0.27	0.31
Wood Thrush (*Hylocichla mustelina*)	1.5	0.09	0.25
American Robin (*Turdus migratorius*)	4.5	0.20	0.40
Cedar Waxwing (*Bombycilla cedrorum*)	2	0.10	0.23
Black-throated Blue Warbler (*Dendroica caerulescens*)	18	1.08	1.46
American Redstart (*Setophaga ruticilla*)	7.5	0.43	1.28
Ovenbird (*Seiurus aurocapillus*)	8	0.46	0.95
Common Yellowthroat (*Geothlypis trichas*)	2	0.06	0.14
Rose-breasted Grosbeak (*Pheucticus ludovicianus*)	5	0.24	0.44
Brown-headed Cowbird (*Molothrus ater*)	9	0.32	0.58

[a] Does not include species found only in one plot or for which less than one full territory was recorded (Table 1).
[b] Positively associated with oldgrowth at landscape level of entire state but not at level of physiographic province.

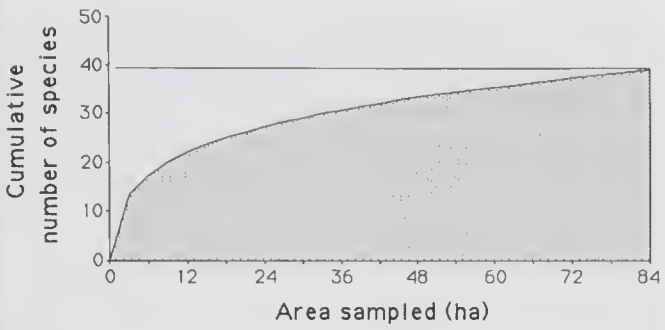

FIG. 1. Mean randomized accumulation curve (1000 iterations) of species richness in the bird community of old-growth conifer-hardwood forest on the northern Appalachian Plateau, Pennsylvania. Horizontal line indicates the putative asymptote of species richness as a function of area sampled. The asymptote was identified with a maximum likelihood estimater.

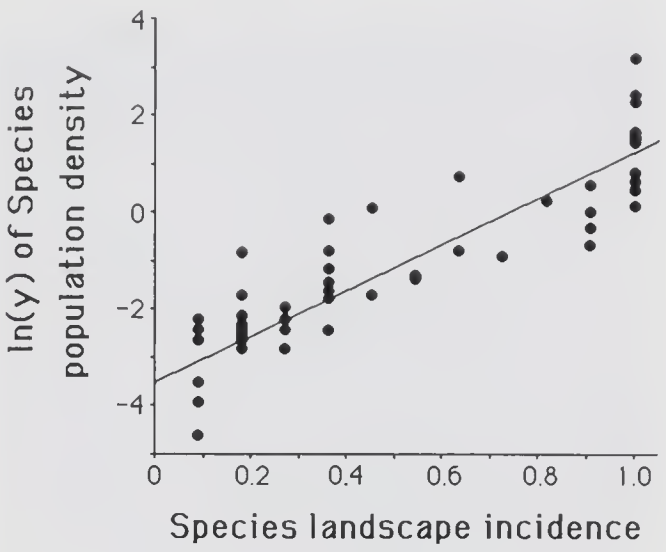

FIG. 2. Relationship between natural log of population density (number of breeding territories) and landscape incidence of all bird species (n = 56) found in old-growth conifer-hardwood forest of the northern Appalachian Plateau, Pennsylvania. Landscape incidence is based on the proportion of old-growth study plots (n = 11; Table 1) in which the species was recorded. Log of population density (y) is related to landscape incidence (x) by: $y = 4.741x - 3.513$, ($r^2 = 0.805$, $P < 0.001$).

ceus), Hooded Warbler (*Wilsonia citrina*), and Scarlet Tanager (*Piranga olivacea*).

Incidence versus population density.—Bird species that were rare or uncommon at landscape levels typically had low population densities locally as well. Incidence explained slightly more than 80% of the variation in the natural log of population size as assessed by territorial density (Fig. 2).

DISCUSSION

Old-growth affinities.—At both province and state levels, more than one-third of bird species were more likely to occur in old-growth conifer-hardwood forest than in the broader landscape. These species included some of Pennsylvania's rarest breeding birds. Yellow-bellied Flycatcher (*Empidonax flaviventris*) and Swainson's Thrush (*Catharus ustulatus*) are listed in the state as threatened and candidate-rare, respectively (D. A. Gross, pers. comm.). Pending investigation of specific habitat preferences for individual species, the 15 birds in this group (Table 2) are best regarded as old-growth associates rather than old-growth obligates. Nevertheless, it is notable that these species have diverse habitat affinities, including conifer [e.g., Red-breasted Nuthatch (*Sitta canadensis*)], hardwood [e.g., Blue-headed Vireo (*Vireo solitarius*)], and mixed forest cover types [e.g., Hairy Woodpecker (*Picoides villosus*)].

Several taxa identified as old-growth associates in this study have been linked repeatedly to late successional forest elsewhere throughout North America. Hairy Woodpeckers rely on mature forests with large snags and logs (Anthony et al. 1996, Shackelford and Conner 1998). Across broad geographic domains, Red-breasted Nuthatch, Brown Creeper (*Certhia americana*), Winter Wren (*Troglodytes troglodytes*), and Golden-crowned Kinglet (*Regulus satrapa*) form a recurring group that exploits coniferous cover and complex structure typical of older natural forests (DeGraaf et al. 1992, Hansen et al. 1995, Schieck et al. 1995, Anthony et al. 1996, Dellasala et al. 1996).

In other cases, regional counterparts of genera exhibited a common tendency to prefer mature forest. Acadian Flycatcher (*Empidonax virescens*) showed a greater likelihood of occurring in mesic old-growth forest relative to adjacent landscapes (Table 1), similar to Hammond's (*E. hammondii*) and Pacific-slope (*E. difficilis*) flycatchers in Oregon and British Columbia (Hansen et al. 1995, Schieck et al. 1995). Like their western congeners Hermit (*Dendroica occidentalis*) and Townsend's warblers (*D. townsendi*; Hansen et al. 1995, Schieck et al. 1995), several species of arboreal *Dendroica* warblers were far more likely to occur in old-growth hemlock-white pine-northern hardwood forest than in adjacent

landscape units (Tables 1 and 2). Populations of Blackburnian Warblers (*D. fusca*) achieve particularly high densities in the oldest conifer-hardwood forests of this region (Haney and Schaadt 1996: fig. 6.1).

Two species, Red-shouldered Hawk and Barred Owl, were more likely to occur in old-growth than across the state as a whole (Table 1). Red-shouldered Hawks depend on mature forests with large trees for nest sites (Titus and Mosher 1981, Moorman and Chapman 1996). Barred Owls exhibit greater territorial occupancy and breeding propensity in this region's old-growth forest (Haney 1997).

Despite directional biases in comparisons of incidence across spatial scales (see *Sampling adequacy*), negative associations of bird species with oldgrowth may have had biological causes. Mourning Dove (*Zenaida macroura*), Blue Jay (*Cyanocitta cristata*), American Crow, and Brown-headed Cowbird (*Molothrus ater*; Table 2) all typically exploit landscapes with extensive anthropogenic disturbance (Martin 1988, Hoover and Brittingham 1993, Seitz and Zegers 1993, Rodenhouse et al. 1995). Consequently, they would be less expected to occur in mature tracts of reserved forest. Least Flycatcher (*Empidonax minimus*), Black-throated Blue Warbler, American Redstart (*Setophaga ruticilla*), and Rose-breasted Grosbeak (*Pheucticus ludovicianus*) more commonly exploit the deciduous habitats (Sherry and Holmes 1988, Steele 1993, Yahner 1993) typical of younger, regenerating forest now prevalent in this region (Alerich 1993). Ovenbirds (*Seiurus aurocapillus*) were probably scarce because of their preference for heavy ground cover (Burke and Nol 1998), a microhabitat virtually absent in the old-growth forest studied here.

Sampling adequacy.—Deletion of peripheral species and analysis of the asymptote on the species accumulation curve gave similar values for total species: 42 and 39 species, respectively. I conclude that census effort was adequate for characterizing the avian community in old-growth hemlock-white pine-northern hardwood forest on Pennsylvania's northern Appalachian Plateau. Numerical analyses indicated that the community sampled was in fact homogenous and an asymptotic limit to species richness (S_{max}) was achieved with little more than half the sampling effort actually undertaken (Fig. 1). Support for sampling adequacy is reassuring because limited amounts and local distributions of eastern old-growth forest often preclude obtaining larger sample sizes and greater sample dispersion in this scarce habitat type.

Use of bird species richness (S or S_{max}) to evaluate avian habitat can be problematic unless studies account for: (1) "core" members of the avifauna, (2) quantity and quality of sampling effort, (3) number of habitat types within areas, and (4) proximity of other habitats (Remsen 1994, Elphick 1997). The BBC method itself purposefully discounts non-territory holders, thereby eliminating nonbreeding species. I also established study plots within interiors of old-growth forest so as to avoid inflating or confounding species richness caused by proximity of different habitat patch types (Flather 1996).

Although BBC and BBA methods have distinct purposes and can have different quantities and qualities of observer effort, several factors facilitated comparisons of data from the two techniques in this study. First, species occurrence data from both methods were comparable by developing a common incidence metric. Second, both methods rely to some extent upon a measure of saturation in the cumulative number of species recorded in order to guage whether sampling is adequate. Third, both methods had similar levels of observer effort as measured by survey duration. All BBCs took 16.7–20.1 h to complete versus an average of 17 field-h per atlas block (Brauning 1992).

The BBC method's reliance on three or more records to score territorial occupancy, however, is more restrictive in tallying species occurrences than the BBA method. The latter includes "possible," "probable," and "confirmed" categories of breeders, and is therefore likely to include more species per unit effort. Greater numbers of species may also be detected with the BBA method because of the substantially larger areas covered (potentially hundreds or thousands of ha per block versus the tens of ha in most BBCs).

As a consequence of differences in the scope of effort between BBC and BBA methods, comparisons of incidence values (I) for individual species (Table 1) may be biased against detecting greater occurrence (and to-

wards detecting lower occurrence) in oldgrowth habitat than in the landscape at large. Findings of positive old-growth association by individual species (Table 2) are more robust as a result. Negative and neutral associations with oldgrowth should be interpreted cautiously because more liberal listing of species under BBA methodology could elevate relative incidence values at state and province levels, thereby leading to false conclusions that no differences in species occurrences existed across spatial scales (Type II error).

Hierarchical comparisons.—Although scale is viewed as essential for interpreting distributional data in birds (Lacy and Bock 1986), logistical constraints and methodological inconsistencies often prevent hierarchical or multi-tiered approaches. Comparing local density of bird populations to density in a region as large as an entire state is impossible because the BBC method requires large investments in time for limited spatial coverage. Proportions are easy to derive from virtually any kind of sample, however, and a metric based on incidence enabled direct comparison of species occurrences in BBC plots and atlas blocks (Table 1).

Comprehensive coverage in Pennsylvania's atlas program also enabled more reliable comparisons of birds in oldgrowth to the wider landscape: all blocks, including those on the state's borders, were censused (Brauning 1992). Synoptic coverage allows evaluation of the likely impacts of potential actions on groups of bird species within a wider context. It would be easy to scale down from the ecophysiographic province or state levels used in this study to some smaller region of interest (e.g., county, national forest, watershed). Alternatively, BBA data from adjacent states could be aggregated to examine individual species occurrences across even larger landscape units. This spatial flexibility should enable better evaluation of potential consequences of local management prescriptions on the regional distributions of birds.

I used an incidence metric as a reasonable proxy for population size (Fig. 2). Several researchers have documented a general relationship between abundance and range size in birds (Bock and Ricklefs 1983, Lacy and Bock 1986, Mauer and Heywood 1993). This relationship may not indicate the existence of a particular ecological hypothesis (Wright 1991). Nevertheless, the generality that species with sparse distributions also have low population densities was confirmed in this study by documenting regional scarcity in several bird species that use a rare and very local habitat type.

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EFFECTS OF WIND TURBINES ON UPLAND NESTING BIRDS IN CONSERVATION RESERVE PROGRAM GRASSLANDS

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ABSTRACT.—Grassland passerines were surveyed during summer 1995 on the Buffalo Ridge Wind Resource Area in southwestern Minnesota to determine the relative influence of wind turbines on overall densities of upland nesting birds in Conservation Reserve Program (CRP) grasslands. Birds were surveyed along 40 m fixed width transects that were placed along wind turbine strings within three CRP fields and in three CRP fields without turbines. Conservation Reserve Program grasslands without turbines and areas located 180 m from turbines supported higher densities (261.0–312.5 males/100 ha) of grassland birds than areas within 80 m of turbines (58.2–128.0 males/100 ha). Human disturbance, turbine noise, and physical movements of turbines during operation may have distrurbed nesting birds. We recommend that wind turbines be placed within cropland habitats that support lower densities of grassland passerines than those found in CRP grasslands. *Received 9 Sept. 1997, accepted 5 Oct. 1998.*

Technological advances that have reduced the cost of electricity generated from windplants have enabled the wind-power industry to expand from California into the eastern United States and Canada (Nelson and Curry 1995). Wind power has received strong public support as an alternative energy source despite the potential threats that the presence of wind turbines may pose to avian species. Recent research has indicated that raptor mortality from collisions with wind turbines varies greatly from no mortality (Higgins et al. 1996; Usgaard et al., in press) to substantial mortality (Orloff and Flannery 1992). In addition to direct mortality from collisions, research also has indicated that waterfowl, wading bird, and raptor densities near turbines were lower compared to densities in similar habitats away from turbines (Winkelman 1990; Pedersen and Poulsen 1991; Usgaard et al., in press). The influence of wind turbines on grassland nesting passerine species has not been previously measured.

Recent construction of the first windplant facility in the midwestern United States provided a unique opportunity to study the effects of wind turbines on grassland nesting passerines. Several midwestern grassland passerine species have declined in abundance (Johnson and Schwartz 1993) in response to agricultural tillage, grazing, and invasive woody species that have destroyed or degraded most of the remaining grasslands (Kantrud 1981, Castrale 1985). Although Conservation Reserve Program (CRP; Young and Osborn 1990) grasslands provide habitat for grassland nesting birds (Johnson and Schwartz 1993, Igl and Johnson 1995, Johnson and Igl 1995, King and Savidge 1995, Millenbah et al. 1996), the potential impact of wind turbines in CRP fields could negate those benefits. The objective of this study was to determine whether density of upland nesting passerines in CRP grasslands was influenced by the presence of wind turbines. We hypothesized that bird density in CRP grasslands would not differ in relation to distance from wind turbines.

STUDY AREA AND METHODS

Study area.—The Buffalo Ridge Wind Resource Area (WRA) in southwestern Minnesota is located along a 100 km segment of the Bemis Moraine near Lake Benton, Minnesota. Elevation is 546–610 m. Wind turbines cover 32 km^2 of the 293 km^2 Buffalo Ridge WRA. Additional lands within the Buffalo Ridge WRA have been leased as future wind-turbine development sites. The windplant contains 73 operational wind turbines that are arranged in 10 turbine strings, with 3–20 turbines/string. Turbines are 91–183 m apart within strings. Turbines (model KVS-33; KENETECH Windpower, Inc.), which operate at wind speeds of 14–104 km/h, consist of a 33 m diameter rotor mounted on a 37 m tubular tower.

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Upland grassland bird nesting habitat within the Buffalo Ridge WRA consisted primarily of CRP grasslands, mostly planted with a mixture of smooth brome (*Bromus inermis*) and alfalfa (*Medicago sativa*) or switchgrass (*Panicum virgatum*). Habitats surrounding CRP grasslands were agricultural lands dominated by corn (*Zea mays*) and soybeans (*Glycine max*) with smaller areas of haylands, pasturelands, and scattered woodlands near farmsteads and in ravines.

Methods.—Bird survey transects were placed along wind-turbine strings within three CRP fields and in three CRP fields without turbines (i.e., control; Leddy 1996). We selected CRP fields that were 7–8 years of age to minimize effects of field age on diversity and density of avain species (Millenbah et al. 1996). Visual obstruction readings (Robel et al. 1970, Higgins and Barker 1982) did not differ between CRP grasslands with and without turbines, indicating that vegetation structure in experimental and control fields was similar (Leddy 1996). Transects were surveyed weekly in random order from 15 May to 1 July 1995. Multiple surveys of a single transect were averaged into one bird density to avoid pseudoreplication (Hurlbert 1984). Six 40-m fixed width transects (Wakeley 1987) paralleling each turbine string were used per field. One transect ran directly underneath turbine strings. Two additional transects on each side of the turbine string paralleled the string at distances of 40 and 80 m; the sixth transect was placed 180 m from the turbine string. Transects varied in length according to field size and were placed at least 30 m from field borders and wetlands to minimize bias associated with edges (Arnold and Higgins 1986, Reese and Ratti 1988). One transect was established at a random location in each of the three control CRP fields without turbines.

Inconsistencies among surveys attributable to periodic bird inactivity (Skirvin 1981, Verner and Ritter 1986) were minimized by conducting surveys from sunrise to 10:00 CST. We recorded all birds seen or heard while walking transects at 1.0–1.5 km/h (Mikol 1980, Wakeley 1987); only perched and/or singing males were used in statistical analyses. Flushed birds seen leaving transects were counted (Burnham et al. 1980), whereas birds seen entering transects or flying overhead were not counted. Surveys were not conducted during heavy rain or high winds (≥20 km/h; Ralph et al. 1993). Birds were surveyed in CRP fields with turbines when turbines were operational and non-operational because turbines began operating during surveys when wind speeds reached 14–20 km/h. We compared surveys that were conducted during operational and non-operational periods to determine whether noise produced during turbine operation biased surveys.

An index of total breeding bird density was calculated by dividing the number of perched and/or singing males by transect area. Percent species composition was calculated by dividing the number of perched and/or singing males of a particular species by the total number of males. Species richness was defined as the number of species (Koford et al. 1994).

Analysis of covariance (SAS 1989) was used to determine whether bird density across transects was related to noise produced during wind turbine operation. We used turbine operational status (i.e., running versus idle) to determine whether the slope of bird densities differed. Analysis of variance (ANOVA; SAS 1989) was used to determine whether bird density in CRP grasslands without turbines differed from that in CRP grasslands containing turbines. An ANOVA also was used to determine whether bird density was related to distance from wind turbines. A Least Significant Difference Multiple Comparisons test was used to determine where differences in bird density occurred among transects.

RESULTS

Ten upland grassland bird species occurred in CRP grasslands with and without turbines (Table 1). Bobolinks (*Dolichonyx oryzivorus*), Red-winged Blackbirds (*Agelaius phoeniceus*), and Savannah Sparrows (*Passerculus sandwichensis*) comprised 74.5% of the birds in CRP grasslands with turbines (Table 1). Bobolinks, Sedge Wrens (*Cistothorus platensis*), and Savannah Sparrows comprised 80.0% of the individuals in CRP fields without turbines (Table 1).

Mean bird densities from surveys conducted while wind turbines were operational ($\bar{x}$ = 4.7 ± 0.88 SE) and non-operational ($\bar{x}$ = 5.4 ± 0.94 SE) were pooled because slopes of bird densities among transects did not differ (F = 0.39, 1,30 df, $P > 0.05$). Total bird density was lower in CRP grasslands containing turbines than in CRP grasslands without turbines (F = 17.36, 6,14 df, P = 0.001; Table 2). Bird density was lower (F = 12.37, 1,10 df, P = 0.006) in the 0 and 40 m transects compared to density in transects 80 m or more from turbines (Table 2). Bird density also was lower (F = 13.10, 1,10 df, P = 0.001) in transects within 80 m of the turbines compared to 180 m from turbines (Table 2). Bird density 180 m from turbines did not differ (F = 0.10, 1,10 df, $P > 0.05$) from that in CRP grasslands without turbines (Table 2). A linear relationship existed (r^2 = 0.746, n = 18, $P < 0.001$) between bird density and transect distance from turbines (Fig. 1).

DISCUSSION

Conservation Reserve Program grasslands without turbines and areas located 180 m from turbines supported mean densities of grassland birds that were four times higher than those

TABLE 1. Number (*n*) and percent (%) composition of breeding grassland birds in Conservation Reserve Program grasslands with and without turbines at the Buffalo Ridge Wind Resource Area, Minnesota, May–July 1995.

Species	Turbines		No turbines	
	n	%	*n*	%
Bobolink (*Dolichonyx oryzivorus*)	139	36.6	48	32.0
Red-winged Blackbird (*Agelaius phoeniceus*)	85	22.4	7	4.7
Savannah Sparrow (*Passerculus sandwichensis*)	59	15.5	33	22.0
Common Yellowthroat (*Geothlypis trichas*)	36	9.5	7	4.7
Dickcissel (*Spiza americana*)	22	5.8	2	1.3
Le Conte's Sparrow (*Ammodramus leconteii*)	10	2.6		
Brown-headed Cowbird (*Molothrus ater*)	9	2.4	6	4.0
Western Meadowlark (*Sturnella neglecta*)	5	1.3	1	0.7
Grasshopper Sparrow (*Ammodramus savannarum*)	4	1.1	4	2.7
Sedge Wren (*Cistothorus platensis*)	1	0.3	39	26.0
Clay-colored Sparrow (*Spizella pallida*)			1	0.7
Unknown	9	2.3	2	1.3
Total species	10		10	

in grasslands nearer to turbines. Three of four species that composed at least 74.5% of the bird community composition (Bobolink, Savannah Sparrow, Sedge Wrens) in CRP fields with and without turbines are area-sensitive species (Herkert 1994a, b; Swanson 1996) that require large tracts of tall, dense vegetation for nesting (Wiens 1969, Herkert 1994a). Minor differences in overall bird species richness and composition were likely related to subtle structural differences in grassland stand types. Leddy and coworkers (in press) found that Clay-colored Sparrows (*Spizella pallida*) and Sedge Wrens using CRP grasslands on the Buffalo Ridge WRA preferred dense stands of switchgrass while Dickcissels (*Spiza americana*) and Bobolinks usually used stands of smooth brome and alfalfa.

TABLE 2. Species richness and mean density of upland grassland birds/100 ha at varying distances from wind turbines in Conservation Reserve Program grasslands at the Buffalo Ridge Wind Resource Area, Minnesota, May–July 1995.

Transect	*n*	Breeding males		
		Species richness	Mean density[a]	SE
0 m	3	6	58.2 A	26.3
40 m	6	8	66.0 A	17.1
80 m	6	7	128.0 B	19.6
180 m	3	9	261.0 C	12.0
CRP Control	3	10	312.5 C	15.7

[a] Means denoted by the same letter do not differ ($P \leq 0.05$).

Little evidence has been found linking avian mortality to collisions with wind turbines on the Buffalo Ridge WRA (Higgins et al. 1996). Although wind turbines may not directly cause mortality, the presence of wind turbines may indirectly affect local grassland bird populations by decreasing the area of grassland habitat available to breeding birds. Comparison of bird density and species richness among transects indicated that bird use of grasslands 180 m from turbines was similar to that in CRP fields without turbines (Table 2). Although research in the Netherlands also

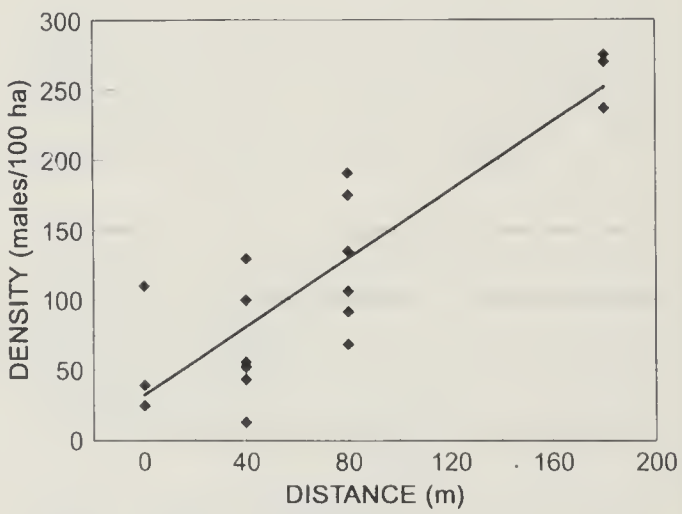

FIG. 1. Linear relationship (Density = 32.30 + 1.22 × Distance; $r^2 = 0.746$) between breeding bird density (males/100 ha) and distance (0–180 m) from wind turbines in Conservation Reserve Program grasslands at the Buffalo Ridge Wind Resource Area in southwestern Minnesota, May–July 1995.

has indicated that the presence of turbines has prevented waterfowl and wading bird species from using otherwise suitable habitat (Winkelman 1990, Pedersen and Poulsen 1991), mechanisms inhibiting birds from exploiting grasslands near turbines have not yet been identified. In addition to human disturbance and noise, the physical movements of the turbines when they are operating may have disturbed nesting birds. Maintenance trails between turbines that are driven daily may have further decreased the availiability of grassland habitat adjacent to turbines.

Construction of windplants within midwestern grassland habitats may soon become an additional source of habitat degradation as demands for wind generated power increase. Current grazing and tillage practices on many privately owned lands that are less conducive to grassland bird production increase the importance of remaining grasslands to prairie nesting birds (Johnson and Schwartz 1993; Johnson and Igl 1995; Leddy et al., in press). Until additional research is conducted, we recommend that wind turbines be placed within cropland habitats that support lower densities of grassland passerines than those found in CRP grasslands (Leddy et al., in press). We also recommend that additional research be conducted in other geographic regions where wind generated power is currently used to further assess possible effects of wind turbines on avian habitats.

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AVIAN USE OF PURPLE LOOSESTRIFE DOMINATED HABITAT RELATIVE TO OTHER VEGETATION TYPES IN A LAKE HURON WETLAND COMPLEX

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ABSTRACT.—Purple loosestrife (*Lythrum salicaria*), native to Eurasia, is an introduced perennial plant in North American wetlands that displaces other wetland plants. Although not well studied, purple loosestrife is widely believed to have little value as habitat for birds. To examine the value of purple loosestrife as avian breeding habitat, we conducted early, mid-, and late season bird surveys during two years (1994 and 1995) at 258 18-m (0.1 ha) fixed-radius plots in coastal wetlands of Saginaw Bay, Lake Huron. We found that loosestrife-dominated habitats had higher avian densities, but lower avian diversities than other vegetation types. The six most commonly observed bird species in all habitats combined were Sedge Wren (*Cistothorus platensis*), Marsh Wren (*C. palustris*), Yellow Warbler (*Dendroica petechia*), Common Yellowthroat (*Geothlypis trichas*), Swamp Sparrow (*Melospiza georgiana*), and Red-winged Blackbird (*Agelaius phoeniceus*). Swamp Sparrow densities were highest and Marsh Wren densities were lowest in loosestrife dominated habitats. We observed ten breeding species in loosestrife dominated habitats. We conclude that avian use of loosestrife warrants further quantitative investigation because avian use may be higher than is commonly believed. *Received 27 May 1998, accepted 26 Aug. 1998.*

Purple loosestrife (*Lythrum salicaria*) is an exotic, broad-leaved, herbaceous perennial that is common in North American freshwater wetland habitats north of 35° N latitude (Thompson 1989). Loosestrife is native to Eurasia where it occurs in freshwater marshes, open stream margins, and alluvial floodplains; it invades similar habitats in North America (Thompson 1989). Common plant associates of loosestrife in North American wetland habitats such as cattails (*Typha* spp.), reed canary grass (*Phalaris arundinacea*), sedges (*Carex* spp.), and rushes (*Juncus* spp.) closely resemble its associates in Eurasian wetlands (Thompson et al. 1987). Loosestrife out competes and partially or completely replaces native emergent vegetation (Thompson 1989). Loosestrife often pioneers in disturbed areas such as drainage ditches (Wilcox 1995) and displaces moist-soil species such as smartweeds (*Polygonum* spp.) and millets (*Panicum* spp.) on mudflats (Thompson et al. 1987). Species of wetland plants become distributed along a wetland gradient and are good indicators of long-term hydrology and other abiotic factors (Keddy and Reznicek 1985). Wetland vegetation types generally grade from forested wetland to shrub-scrub, to wet meadow, to strand (or mudflat), to emergent marsh, and finally, to open water (Cowardin et al. 1979, Keddy and Reznicek 1985). Loosestrife occupies zones near the strand including emergent and wet meadow zones.

Avian use of loosestrife is not well studied (Thompson et al. 1987). Prince and Flegel (1995) found no records in the literature of loosestrife as avian food or nesting habitat in Lake Huron wetlands. In New York wetlands, Rawinski and Malecki (1984) observed that Marsh Wrens (*Cistothorus palustris*) preferred cattail for nesting, whereas Red-winged Blackbirds (*Agelaius phoeniceus*) preferred loosestrife for nesting. Rawinski and Malecki (1984) also noted that Black-crowned Night-herons (*Nycticorax nycticorax*) roosted in loosestrife, and Pied-billed Grebes (*Podilymbus podiceps*) nested in one- and two-year-old emergent loosestrife stands. Kiviat (1996) found 15 American Goldfinch (*Carduelis tristis*) nests in loosestrife during a 23-year study of birds in the Hudson Valley. Swift and coworkers (1988) observed Least Bitterns (*Ixobrychus exilis*) and other birds in Hudson River wetlands that consisted of cattail, river bulrush (*Scirpus fluviatilis*), loosestrife, and common reed (*Phragmites australis*).

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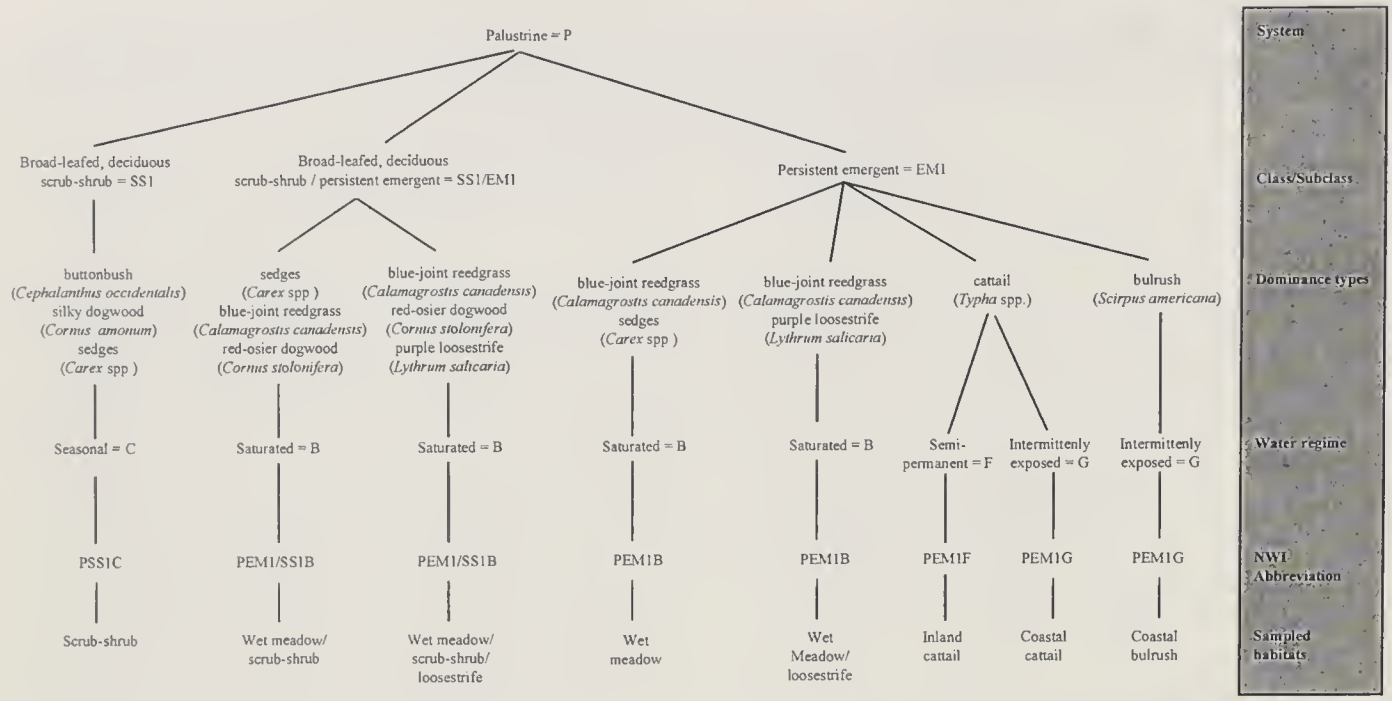

FIG. 1. Characteristics of surveyed vegetation types in Saginaw Bay wetlands, 1994–1995, based on National Wetlands Inventory (Cowardin et al. 1979) classification system. PSS1C = Palustrine, broad-leafed deciduous scrub-shrub, and seasonally flooded; PEM1/SS1B = Palustrine, persistent emergent/broad-leafed deciduous scrub-shrub, and saturated; PEM1B = Palustrine, persistent emergent, and saturated; PEM1F = Palustrine, persistent emergent, and semi-permanently flooded; PEM1G = Palustrine, persistent emergent, and intermittently exposed (Cowardin et al. 1979).

Minnesota established the first statewide loosestrife control program in 1987 with the goal of broadening public awareness, conducting inventories, developing control methods, and initiating control work (Skinner et al. 1994). Minnesota has spent $US 1.75 million since the beginning of the program (Skinner, pers. comm.). Other state and federal agencies also have spent considerable money and effort to control loosestrife, in part, because wildlife values of this plant are widely regarded to be limited. Methods of control have included use of chemicals, water manipulation, mowing, tillage, planting robust mudflat species such as Japanese millet (Thompson 1989), and, most recently, biological control using insects (Malecki et al. 1993).

Our objective was to compare avian use of vegetation zones dominated by loosestrife with other wetland zones where loosestrife was absent or not dominant. Comparison of avian breeding species richness, density, and diversity is a necessary first step to assess the value of loosestrife-dominated habitats to birds, and ultimately to evaluate costs and benefits of loosestrife control.

METHODS

We conducted field work during 1994 and 1995 in Bay, Tuscola, and Huron counties adjacent to Saginaw Bay, Lake Huron, Michigan. Saginaw Bay comprises the majority of remaining wetland habitat on Lake Huron because unsuitable shore morphology (e.g., cliffs) prohibited wetland formation, and development pressures (mostly agricultural) eliminated presettlement wetland habitats (Prince and Flegel 1995). Although this area has experienced a 50% overall wetland loss (Dahl 1990), 70% of inland wetlands and 99% of lakeplain prairies have been drained and converted to other uses (Comer 1996). Most existing Saginaw Bay wetlands are disturbed by adjacent urban and agricultural development, diking, and exotic flora and fauna.

We surveyed birds on 18-m fixed-radius plots in eight vegetation types based on hydrology and plant form and structure: scrub-shrub, wet meadow/scrub-shrub, wet meadow/scrub-shrub/loosestrife, wet meadow, wet meadow/loosestrife, inland cattail, coastal cattail, and coastal bulrush (*Scirpus* spp.). Our habitat classifications were based on Cowardin and coworkers (1979); dominant plants had greater than 30% cover (Fig. 1). We used a split class (e.g., broad-leafed deciduous scrub-shrub/persistent emergent; National Wetlands Inventory) to classify two vegetation types because scattered shrubs of at least 30% cover were present. We separated cattail sites into coastal and inland because hydrologies differed; coastal sites were

TABLE 1. Mean cover (Robel) height (cm) ± SE and mean water depth (cm) ± SE by period and vegetation type in Saginaw Bay wetlands, 1994–1995.

	Period 1		Period		Period 3	
Year and site[a]	Cover height	Water depth	Cover height	Water depth	Cover height	Water depth
1994 SS	27.8 ± 4.3	27.5 ± 0.9	55.0 ± 5.9	12.1 ± 3.2	75.7 ± 8.1	25.4 ± 2.9
1995 SS	35.8 ± 3.4	24.4 ± 0.8	68.8 ± 4.3	14.4 ± 0.7	74.6 ± 5.5	1.9 ± 0.6
1994 WM/SS	—[b]	—	62.8 ± 4.2	saturated	56.7 ± 3.5	saturated
1995 WM/SS	24.4 ± 4.1	0.2 ± 0.2	67.8 ± 7.8	saturated	100.8 ± 8.7	saturated
1994 WM/SS/LS	—	—	107.5 ± 11.0	saturated	101.1 ± 3.9	saturated
1995 WM/SS/LS	30.0 ± 8.5	saturated	48.9 ± 4.2	saturated	87.8 ± 9.5	0.5 ± 1.7
1994 WM/LS	—	—	84.4 ± 8.8	saturated	106.7 ± 8.2	2.2 ± 0.4
1995 WM/LS	38.9 ± 4.8	saturated	63.3 ± 3.3	saturated	87.8 ± 6.4	saturated
1994 WM	—	—	81.7 ± 5.1	0.3 ± 0.2	83.9 ± 2.6	1.8 ± 0.8
1995 WM	30.6 ± 2.6	saturated	61.1 ± 4.3	saturated	68.3 ± 6.7	saturated
1994 IC	80.0 ± 3.2	29.9 ± 2.0	70.7 ± 4.1	21.0 ± 1.7	110.6 ± 7.2	26.4 ± 1.4
1995 IC	41.4 ± 6.6	17.1 ± 3.4	52.4 ± 9.0	13.3 ± 2.5	94.8 ± 6.4	7.7 ± 1.9
1994 CC	—	—	71.2 ± 7.5	22.0 ± 2.6	144.3 ± 8.2	31.6 ± 2.4
1995 CC	60.3 ± 4.7	9.1 ± 1.4	82.2 ± 6.3	12.5 ± 1.5	127.9 ± 8.3	22.2 ± 1.7
1994 CB	—	—	11.3 ± 3.4	33.5 ± 1.4	34.7 ± 5.5	36.8 ± 1.2
1995 CB	—	—	8.9 ± 2.7	23.7 ± 0.8	33.2 ± 3.6	30.1 ± 1.1

[a] Vegetation types: SS = scrub-shrub, WM/SS = wet meadow/scrub-shrub, WM/SS/LS = wet meadow/scrub-shrub/loosestrife, WM/LS = wet meadow/loosestrife, WM = wet meadow, IC = inland cattail, CC = coastal cattail, CB = coastal bulrush.
[b] Dashes (—) indicate insufficient or lack of data.

intermittently exposed, whereas inland sites were semipermanently flooded by groundwater and precipitation.

Sampling periods were divided into an early season during the second and third weeks of May, a midseason during the first and second weeks of June, and a late season during the last week of June and first week of July. We conducted surveys between sunrise and 10:00 EST. Surveys were not conducted if sustained winds exceeded 24 km/h or during heavy rain.

We selected plots using the following protocol: first, an azimuth was determined that traversed the habitat. The center of the first plot was placed at least 18 m from the outer boundary of the vegetation on that azimuth. The center of the next plot was 70 m from the first plot on the same azimuth. This procedure was continued until observers surveyed three or more plots or reached a different vegetation type. If fewer than 3 plots were established on the first azimuth, we established a second azimuth, approximately perpendicular to the first azimuth, that traversed the vegetation type and permitted plot placement at least 70 m from other plots. Plots were set on this azimuth in the same manner as on the first azimuth. Plots were placed in different locations at the same site among time periods to avoid resampling the same plots and recounting the same nests. Coastal bulrush plots were not surveyed during the first periods of each year because they lacked structure; new vegetative growth was not yet established and the previous year's growth was eliminated by ice action. Neither did we survey three vegetation types (wet meadow/scrub-shrub/loosestrife, wet meadow, wet meadow/loosestrife) during the first period of 1994. We surveyed 258 plots in 8 wetland habitats.

Observers waited 5 min for normal bird activity to resume after arriving at a survey plot. We recorded all birds seen or heard on plots during a 7-min observation period. We recorded flying birds if their flight originated or terminated within the plot and we tallied individual birds only once. We played tape-recorded calls (Peterson 1990) of five secretive species [American Bittern (*Botaurus lentiginosus*), Least Bittern, King Rail (*Rallus elegans*), Virginia Rail (*R. limicola*), and Sora (*Porzana carolina*)] during the last 3 min using portable cassette recorders (Johnson et al. 1981, Marion et al. 1981, Johnson and Dinsmore 1986). We played calls for 25–30 sec followed by 10 sec of silence. We measured water depth and vertical cover 4 m from the plot center at 0°, 120°, and 240° (Table 1). Observers measured vertical cover to the nearest 10 cm using a 2-m Robel pole placed at plot center and viewed while maintaining eye level 1 m above the water surface or ground level and looking back toward plot center (Higgins et al. 1994). Workers returned to plots later that day and searched the innermost 13-m radius (0.05 ha) portion for nests. A bird species was designated as breeding when nests or flightless young were observed in one or more periods or when adults were observed in two of three periods (Brown and Dinsmore 1986). A nest verified breeding status when eggs, young, or strong evidence of use such as egg shell fragments, down, or fecal sacs were present. We considered predated nests as breeding evidence when prey species could be determined. We also tallied species as breeding if they were observed within the sampled vegetation type but outside of plot boundaries on two of three visits.

We tallied breeding species richness (i.e., number of breeding species) for each vegetation type. We calculated avian diversities for each plot using the Shannon-

TABLE 2. Distribution of breeding birds by vegetation type in Saginaw Bay wetlands, 1994–1995. Breeding status based on observation of adults on at least two of three visits, or a nest or flightless young on at least one visit.

Species	SS[a]	WM/SS[a]	WM/SS/LS[a]	WM/LS[a]	WM[a]	IC[a]	CC[a]	CB[a]
Pied-billed Grebe[b]							X	X
American Bittern				X		X		
Least Bittern						X	X	
Canada Goose						X	X	
Wood Duck[b]	X							
American Black Duck	X							
Mallard	X	X	X	X	X	X		
Blue-winged Teal			X		X			
Redhead[b]						X		
Northern Harrier[b]		X						
Ring-necked Pheasant		X			X			
Virginia Rail	X		X	X		X	X	
Sora	X					X	X	
Common Moorhen/American Coot[c]						X	X	X
Forster's Tern[b]							X	
Black Tern[b]						X	X	
Northern Flicker	X							
Eastern Wood-pewee	X							
Willow Flycatcher		X						
Great Crested Flycatcher	X							
Eastern Kingbird	X				X			
Tree Swallow	X	X						
Sedge Wren		X	X		X			
Marsh Wren						X	X	
Gray Catbird	X	X						
Yellow Warbler	X	X	X					
Common Yellowthroat	X	X	X		X	X	X	
Rose-breasted Grosbeak	X							
Savannah Sparrow		X			X			
Song Sparrow	X	X						
Swamp Sparrow	X	X	X	X	X	X	X	
Bobolink		X						
Red-winged Blackbird	X		X	X	X	X	X	
Yellow-headed Blackbird							X	
Brewer's Blackbird	X							
Brown-headed Cowbird	X	X						
Baltimore Oriole	X							
American Goldfinch		X	X					
Total	20	15	9	5	9	13	13	2

[a] Vegetation types: SS = scrub-shrub, WM/SS = wet meadow/scrub-shrub, WM/SS/LS = wet meadow/scrub-shrub/loosestrife, WM/LS = wet meadow/loosestrife, WM = wet meadow, IC = coastal cattail, CB = coastal bulrush.

[b] Species observed within the sampled vegetation type but not on plots.

[c] American Coot and Common Moorhen were grouped together because these species were most often observed by call only and their calls are difficult to distinguish.

Weiner diversity index. Density was the number of birds (both sexes) observed on a plot multiplied by 10 to obtain density per hectare.

We used ANOVA (PROC GLM; SAS 1990; SAS 6.12 for Windows) to assess fixed effects of vegetation, period, year, and their interactions on avian density and diversity. Residuals were normally distributed, but variances were not homogeneous because we never observed some species in one or more habitats (resulting in means and variances of zero). However, the overall F-statistic from ANOVA is robust to violations in assumptions of homogeneous variances (Sokal and Rohlf 1981). Early-period observations were eliminated from all analyses because of missing data. We considered plots as the experimental units because we decided *a priori* to restrict our inference to Saginaw Bay wetlands. We used $\alpha = 0.05$ for all statistical comparisons. We initially analyzed fully specified models (all main

effects and interactions included). We fitted each model using a backward, stepwise procedure by eliminating non-significant ($P > 0.05$) effects, beginning with highest-order interactions. Thus, our final models included only significant effects or interactions, and main effects or interactions contained in significant higher-order interactions. We used Fisher's protected least significant difference test to isolate differences among least-square means (LSMEANS, SAS 1990) for significant effects in the ANOVA (Milliken and Johnson 1984). We compared density and diversity of birds in loosestrife-dominated vegetation types (wet meadow/serub-shrub/loosestrife and wet meadow/loosestrife) to those in other vegetation types using orthogonal contrasts (PROC GLM; SAS 1990), and estimated least-square means using estimate statements (PROC GLM; SAS 1990). We developed similar models for abundance of the six most commonly observed bird species: Sedge Wren (*Cistothorus platensis*), Marsh Wren, Yellow Warbler (*Dendroica petechia*), Common Yellowthroat (*Geothlypis trichas*), Swamp Sparrow (*Melospiza georgiana*), and Red-winged Blaekbird.

Standard errors reported are for least-square means (SAS 1990). Because multiple comparison of means with heterogenous variances may be misleading (Sokal and Rohlf 1981), we further examined comparisons of non-zero means to means of zero using confidence intervals. For each mean of zero, we construeted a 90% upper confidence limit after assigning the highest standard deviation associated with any mean in the model. We then compared 90% lower confidence intervals for nonzero means to 90% upper confidence intervals for zero means; we considered failure of these intervals to overlap as statistically significant. Resulting confidence intervals for zero means are likely overestimated, yielding a conservative comparison. We note in tables instances where confidence interval comparisons did not corroborate multiple comparisons using Fisher's least significant difference test.

RESULTS

As the season progressed water depths at coastal sites (coastal cattail and coastal bulrush) increased and those at inland sites decreased while vertical cover generally increased at all sites (Table 1). We surveyed 258 plots and observed 39 breeding bird species in Saginaw Bay wetland habitats (Table 2). Six breeding species were observed in the sampled vegetation type, but not on survey plots: Pied-billed Grebe, Wood Duck (*Aix sponsa*), Redhead (*Aythya americana*), Northern Harrier (*Circus cyaneus*), Forster's Tern (*Sterna forsteri*), and Black Tern (*Chlidonias niger*). We also observed 10 species breeding in loosestrife dominated habitats (Table 2).

Marsh Wren ($n = 20$), Swamp Sparrow ($n = 16$), and Red-winged Blackbird ($n = 21$) were the most commonly observed nests on all plots (Table 3). We observed Mallard, Blue-winged Teal (*Anas discors*), Virginia Rail, and Red-winged Blackbird nests while traversing between plots in loosestrife-dominated vegetation zones, but not on the plots.

Avian density and diversity.—Our final model indicated that avian density differed only in relation to vegetation (ANOVA: $F = 14.45$, df = 7, 181, $P < 0.001$; Table 4). Avian density was higher (orthogonal contrast: $F = 8.87$, df = 1, 181, $P = 0.003$) in loosestrife-dominated vegetation types [46.9 ± 3.8 (SE) birds/ha] than in other vegetation types (34.7 ± 1.6). Avian diversity also differed only in relation to vegetation (ANOVA: $F = 12.76$, df = 7, 181, $P < 0.001$; Table 4). Avian diversity was lower (orthogonal contrast: $F = 4.74$, df = 1, 181, $P = 0.03$) in loosestrife-dominated vegetation types (0.42 ± 0.08) than in other vegetation types (0.60 ± 0.03). Effects of year, period, and all interactions were not significant ($P > 0.05$ for all tests) for both avian density and diversity. Scrub-shrub contained the highest bird species diversity and wet meadow/loosestrife and coastal bulrush the lowest (Table 4).

Species abundance.—The vegetation × period × year interaction was significant (ANOVA: $F = 2.34$, df = 7, 157, $P = 0.03$) in our initial Sedge Wren model. Thus, vegetation related differences in Sedge Wren abundance were not consistent among periods and years (Table 5). Within periods and years, Sedge Wren abundance did not differ (orthogonal contrasts: $P > 0.05$ for all tests) between loosestrife dominated vegetation types and other vegetation types.

Marsh Wren abundance differed among vegetation types (ANOVA: $F = 30.72$, df = 7, 181, $P < 0.001$; Table 5). Marsh Wren abundance was lower (orthogonal contrast: $F = 10.73$, df = 1, 181, $P = 0.001$) in loosestrife-dominated vegetation types (0 ± 1.8) than in other vegetation types (6.2 ± 0.7). Yellow Warbler abundance differed among vegetation types, but differences were not consistent between mid- and late periods (ANOVA: vegetation × period interaction, $F = 2.08$, df = 7, 173, $P = 0.048$; Table 5). The interaction was due to significantly higher ($P < 0.001$) numbers of Yellow Warblers observed in late period scrub-shrub compared

TABLE 3. Number of nests and percent of plots within vegetation types where nests of the three most commonly observed bird species were found in Saginaw Bay wetlands, 1994–1995.

Vegetation type[a]	Marsh Wren	Swamp Sparrow	Red-winged Blackbird	Total plots[b]
SS	0	4 (9%)	13 (30%)	43
WM/SS	0	2 (6%)	0	31
WM/SS/LS	0	2 (12%)	0	16
WM/LS	0	4 (27%)	0	15
WM	0	1 (4%)	3 (11%)	27
IC	8 (23%)	3 (8%)	5 (14%)	35
CC	12 (17%)	0	0	71
CB	0	0	0	20
Total nests	20	16	21	—

[a] Vegetation types: SS = scrub-shrub, WM/SS = wet meadow/scrub-shrub, WM/SS/LS = wet meadow/scrub-shrub/loosestrife, WM/LS = wet meadow/loosestrife, WM = wet meadow, IC = inland cattail, CC = coastal cattail, CB = coastal bulrush.
[b] Includes early, mid-, and late season surveys.

with mid-period scrub-shrub (Table 5). Yellow Warbler abundance did not differ (orthogonal contrast: $P > 0.05$ for both tests) between loosestrife-dominated and other vegetation types in either period. Common Yellowthroat abundance differed among vegetation types (ANOVA: $F = 6.04$, df = 7, 181, $P < 0.001$; Table 5). Common Yellowthroat abundance did not differ (orthogonal contrast: $F = 1.20$, df = 1, 181, $P > 0.05$) between loosestrife-dominated and other vegetation types.

Swamp Sparrow abundance differed among vegetation types (ANOVA: $F = 39.03$, df = 7, 180, $P < 0.0001$; Table 5) and between periods (ANOVA: $F = 6.88$, df = 1, 180, $P = 0.009$). Swamp Sparrow abundance was higher during the late period (19.1 ± 1.1 birds/ha) compared with the mid-period (15.2 ± 1.1 birds/ha). Swamp Sparrow abundance was higher (orthogonal contrast: $F = 133.06$, df = 1, 180, $P < 0.001$) in loosestrife-dominated vegetation types (36.0 ± 2.0) than in other vegetation types (10.8 ± 0.8). Swamp Sparrows accounted for 95% and 65% of the overall avian density at wet meadow/loosestrife and wet meadow/scrub-shrub/loosestrife plots, respectively. Abundance of Red-winged Blackbird differed among vegetation types, but differences were not consistent between mid- and late periods (ANOVA: vegetation × period interaction, $F = 2.14$, df = 7, 173, $P = 0.04$; Table 5). The interaction was due to significantly higher ($P < 0.001$) numbers of Red-winged Blackbirds observed in mid-period scrub-shrub compared with late period scrub-shrub (Table 5). Red-winged Blackbird abundance did not differ (orthogonal contrasts: $P > 0.05$ for both tests) between loosestrife dominated and other vegetation types in either period.

DISCUSSION

Weller and Spatcher (1965), Kantrud and Stewart (1984), and Burger (1985) concluded that plant form and structure, rather than taxonomic composition, play key roles in habitat selection by marsh-nesting birds. The structure of loosestrife consists of stout, wood-like persistent growth and herbaceous new growth, similar to shrubs. Overall, species richness in loosestrife was slightly lower than that in other vegetation types except coastal bulrush (Table 2). Scrub-shrub habitat contained the highest breeding species richness and diversity, but these values may be explained in part by the location of scrub-shrub as an ecotone between forest and emergent wetland. Several scrub-shrub breeding birds were not wetland-dependent species but instead birds of forest edge and gaps such as Northern Flicker (*Colaptes auratus*; Moore 1995), Eastern Wood-pewee (*Contopus virens*; McCarty 1996), Great Crested Flycatcher (*Myiarchus crinitus*; Lanyon 1997), and Brown-headed Cowbird (*Molothrus ater*; Lowther 1993).

Swamp Sparrow nests were most abundant in vegetation types where loosestrife was dominant (Table 3). Reinert and Golet (1986) determined that breeding Swamp Sparrows principally required shallow standing water, low (<1.5 m) dense cover, and elevated song-posts, similar to our loosestrife-dominated sites. Swamp Sparrows constructed nests using fine-stemmed sedges and grasses anchored

TABLE 4. Mean avian density (no./ha) ± SE, avian diversity (Shannon-Weaver) ± SE, and number of second and third period plots by (*n*) vegetation type in Saginaw Bay wetlands, 1994–1995.

Vegetation type[a]	*n*[b]	Density[c]	Diversity[c]
SS	30	51.33 ± 3.4 A	1.05 ± 0.08 A
WM/SS	19	38.95 ± 4.3 BC	0.63 ± 0.10 B
WM/SS/LS	13	44.62 ± 5.2 ABC	0.59 ± 0.12 B
WM/LS	12	49.17 ± 5.4 AB	0.22 ± 0.12 C
WM	21	39.52 ± 4.1 BC	0.62 ± 0.09 B
IC	23	41.74 ± 3.9 ABC	0.74 ± 0.09 B
CC	51	36.27 ± 2.6 C	0.56 ± 0.06 B
CB	20	0.5 ± 4.2 D	0 C

[a] Vegetation types: SS = scrub-shrub, WM/SS = wet meadow/scrub-shrub, WM/SS/LS = wet meadow/scrub-shrub/loosestrife, WM/LS = wet meadow/loosestrife, WM = wet meadow, IC = inland cattail, CC = coastal cattail, CB = coastal bulrush.
[b] Excludes early period surveys because of missing data.
[c] Means within columns followed by the same letter do not differ ($P > 0.05$) as determined by ANOVA and Fisher's least significant difference.

in persistent loosestrife stalks. We also observed Mallard, Blue-winged Teal, Virginia Rail, and Red-winged Blackbird nests at our loosestrife-dominated sites, and found American Bittern, Sedge Wren, Yellow Warbler, Common Yellowthroat, and American Goldfinch breeding based on our criteria. Pied-billed Grebe (Rawinski and Malecki 1984), Least Bittern (Swift et al. 1988), Red-winged Blackbird (Rawinski and Malecki 1984), and American Goldfinch (Kiviat 1996) were observed nesting in loosestrife habitats previous to this study.

Rawinski and Malecki (1984) observed that Marsh Wrens preferred cattail habitats, but Red-winged Blackbirds preferred loosestrife habitats. We also found that nesting Marsh Wrens used cattail habitats, but we observed Red-winged Blackbird nests most frequently in scrub-shrub zones (Table 5). Inconsistencies in vegetation type, period, and year effects (i.e., significant three-way interaction) on Sedge Wren abundance may reflect this species' variable breeding site selection (Table 5). Burns (1982) observed that Sedge Wrens show little site fidelity; this characteristic may be due to the ephemeral nature of wet meadow habitats (Kroodsma and Verner 1978). We believe that Sedge Wren abundance may decline as loosestrife increases in wet meadow canopies. We observed greater areal cover of loosestrife at the wet meadow/loosestrife site compared with the wet meadow/scrub-shrub/loosestrife site and Sedge Wren abundance was significantly higher in two of four sampling periods at the site with less loosestrife (Table 5).

The avian diversity in loosestrife dominated habitats was lower on average than that of other wetland habitats that we surveyed, indicating uneven distributions of fewer species. We found higher avian densities in loosestrife-dominated habitats compared to other vegetation types, although Swamp Sparrows comprised the majority of overall density in loosestrife habitats. Swamp Sparrows accounted for 59% of the overall wet meadow density. Swamp Sparrow densities reported in other studies ranged up to 8.78 individuals/ha (Mowbray 1997) and are considerably lower than our densities in several vegetation types. We observed a significant increase in Swamp Sparrow density between mid- and late periods, which may be explained, in part, by the addition of juveniles from early nests (Peck and James 1987, Beaver 1991, Mowbray 1997). Swamp Sparrows prefer open wetlands of sedges, grasses (i.e., wet meadow), and cattail during the breeding season (Beaver 1991, Mowbray 1997). Principally, loosestrife occurs in the wet meadow, strand, and emergent portions of a typical wetland profile, which are the areas where Swamp Sparrows reach their highest abundance (Beaver 1991, Mowbray 1997).

Nesting female and young Swamp Sparrows satisfy their high protein requirements by consuming invertebrates. Wetherbee (1968) determined that 88% of Swamp Sparrow diets during spring and early summer consisted of insects. Arroll (1995) found that aquatic invertebrate abundance in loosestrife in central Washington was similar to that in cattail and bulrush. Arroll (1995) found only

TABLE 5. Mean density (no./ha) ± SE of the six most commonly observed bird species by vegetation type in Saginaw Bay wetlands, 1994–1995.

	Sedge Wren				
	1994		1995		
Vegetation type[a]	Period 2[b]	Period 3[b]	Period 2[b]	Period 3[b]	Marsh Wren[b]
SS	0 C	0 C	0 B	0 B	0 C
WM/SS	6.7 ± 1.6 B	3.0 ± 1.6 BC	0 B	10.0 ± 1.9 A	0 C
WM/SS/LS	10.0 ± 1.9 AB	0 C	6.7 ± 2.2 A[d]	3.3 ± 2.2 B	0 C
WM/LS	0 C	6.7 ± 2.2 B[e]	0 B	0 B	0 C
WM	13.3 ± 2.2 A	13.3 ± 1.6 A	3.3 ± 1.6 AB	3.3 ± 1.6 B	0.5 ± 1.9 C
IC	0 C	0 C	0 B	0 B	15 .6 ± 1.8 B
CC	0 C	0 C	0 B	0 B	20.6 ± 1.2 A
CB	0 C	0 C	0 B	0 B	0.5 ± 2.0 C

[a] Vegetation types: SS = scrub-shrub, WM/SS = wet meadow/scrub-shrub, WM/SS/LS = wet meadow/scrub-shrub/loosestrife, WM/LS = wet meadow/loosestrife, WM = wet meadow, IC = inland cattail, CC = coastal cattail, CB = coastal bulrush.

[b] Means within columns followed by the same letter do not differ ($P > 0.05$) as determined by ANOVA and Fisher's least significant difference.

[c] Fisher's least significant difference multiple comparisons were not corroborated by 90% confidence interval comparisons with WM/SS/LS and IC (see METHODS).

[d] Fisher's least significant difference multiple comparison were not corroborated by 90% confidence interval comparisons with WM/SS and WM/LS (see METHODS).

[e] Fisher's least significant difference multiple comparison were not corroborated by 90% confidence interval comparisons with WM/LS (see METHODS).

[f] Fisher's least significant difference multiple comparisons were not corroborated by 90% confidence interval comparison with WM/SS, WM/LS, and CB (see METHODS).

[g] Fisher's least significant difference multiple comparisons were not corroborated by 90% confidence interval comparison with WM/SS, WM/LS, and CB (see METHODS).

nine statistically significant results in 111 individual comparisons of aquatic invertebrates associated with macrophyte stems (using stem vacuum), sediment (using sediment core), and the water column (using activity traps). Of the four statistically different comparisons involving loosestrife, two showed higher Diptera and Ostracoda abundance in cattail compared with loosestrife, and two showed higher Copepod abundance in loosestrife compared with cattail (Arroll 1995). Thus, invertebrate food items during the breeding season do not appear limiting in loosestrife habitat, although quantitative data from the Northeast are needed.

Loosestrife is an anathema to wetland managers because it often replaces seed-producing mudflat species managed to attract waterfowl. Water level manipulations such as early season drawdowns encourage loosestrife establishment (Thompson 1989). Loosestrife forms dense stands that are difficult for some bird species to negotiate and this may be especially true for larger birds such as waterfowl or species that walk on the ground such as bitterns and rails. Our study demonstrates that loosestrife may provide suitable habitat for some passerines.

Many researchers have observed that habitat diversity leads to faunal diversity in wetlands (Weller and Spatcher 1965, Weller and Fredrickson 1974, Weller 1978, Kantrud and Stewart 1984, Burger 1985). The highest avian density, diversity, and productivity in marshes occurs where emergent vegetation is interspersed 1:1 with open water (Weller and Spatcher 1965, Weller and Fredrickson 1974, Fredrickson and Reid 1988). Wetland managers manipulate vegetative interspersion in marshes using artificial drawdowns, muskrat management, and other means (Fredrickson and Reid 1988). Kaminski and Prince (1981) observed increased waterfowl density and diversity coincident with increased abundance, biomass, and diversity of macroinvertebrates in manipulated emergent wetland habitat. Our loosestrife sites contained few openings. We suspect that manipulated loosestrife habitat (to create interspersion) could result in higher bird diversity.

Loosestrife was widespread in Saginaw Bay coastal wetlands and dominated canopies at several sites. Although diversity was low, loosestrife provided nesting and brood rearing habitat to birds in Saginaw Bay wetlands where alternative habitat choices were available. Some species, such as Marsh Wren, may be disadvantaged as loosestrife displaces other plant forms (e.g., cattail and bulrush). Swamp Sparrows may prefer loosestrife habitat where

TABLE 5. Extended.

Yellow Warbler		Common Yellowthroat[b]	Swamp Sparrow[b]	Red-winged Blackbird	
Period 2[b]	Period 3[b]			Period 2[b]	Period 3[b]
9.3 ± 1.0 A	14.7 ± 1.0 A	2.7 ± 0.6 B[e]	11.3 ± 1.8 C	17.3 ± 1.8 A	6.0 ± 1.8 A[g]
3.3 ± 1.3 B	2.0 ± 1.2 B	5.3 ± 0.8 A	21.5 ± 2.3 B	0 C	0 B
2.8 ± 1.4 B	1.7 ± 1.6 B	1.5 ± 1.0 BC	27.8 ± 2.8 B	7.1 ± 2.7 B[f]	1.7 ± 2.9 AB
0 B	0 B	0 C	44.2 ± 2.9 A	0 C	0 B
0 B	0 B	1.4 ± 0.8 BC	21.2 ± 2.2 B	6.7 ± 2.4 B[f]	4.2 ± 2.0 AB
0.7 ± 1.0 B	0 B	0 C	9.6 ± 2.1 C	5.7 ± 1.9 BC	4.4 ± 2.4 AB
0 B	0 B	0.2 ± 0.5 C	1.5 ± 1.4 D	1.8 ± 1.4 BC	1.2 ± 1.4 B
0 B	0 B	0 C	0 D	0 C	0 B

nest-building materials (fine-stemmed grasses and sedges) are available. We conclude that avian use of loosestrife warrants further quantitative investigation because avian use may be higher than is commonly believed.

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Short Communications

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Bald Eagle Predation on Common Loon Chick

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ABSTRACT.—We report predation of a Common Loon (*Gavia immer*) chick by an adult Bald Eagle (*Haliaeetus leucocephalus*) in northern Wisconsin. *Received 27 Feb. 1998, accepted 26 Sept. 1998.*

Common Loon (*Gavia immer*) chicks may be vulnerable to aerial and underwater predators, including Bald Eagle (*Haliaeetus leucocephalus*), Common Raven (*Corvus corax*), Herring Gull (*Larus argentatus*), snapping turtle (*Chelydra serpentina*), northern pike (*Esox niger*), and muskellunge (*Esox masquinongy*; Yonge 1981, McIntyre 1988, J. Wilson and M. Meyer, pers. comm.). However, few observers have actually observed such predation (McIntyre 1988). Here we describe the first documented observation of a Bald Eagle killing a loon chick.

On 26 July 1996, while collecting data on parental effort on a pair of color-marked adult Common Loons at the Turtle Flambeau Flowage in north central Wisconsin (46° 0′ N, 90° 10′ W), we observed an adult Bald Eagle capture a 15 day-old loon chick. Loon chicks are most prone to predation during the first two weeks after hatching, but continue to be vulnerable up to 4–5 weeks of age (Yonge 1981, McIntyre 1983, pers. obs.). At 10:00 CST an adult eagle circled the territory several times before perching near the top a lone, 8 m tall tamarack (*Larix laricina*) on a small island (0.1 ha). An adult eagle(s) had been observed within the loons' territory on 2 previous occasions (19, 22 July). When the resting adult loons saw the eagle, they wailed and tremoloed several times. The chick, initially with the adults, disappeared from our sight, apparently beneath some overhanging alder (*Alnus* sp.) along the island's edge. By 10:20 the adult loons stopped vocalizing; the male resumed foraging dives, and the female remained alert on the surface. However, at 10:30, two non-resident loons intruded on the established pair's territory, triggering aggressive interactions for 10–12 min until the intruding pair left the area. The territorial adults remained alert on the surface with the chick still out of sight.

At 10:58 the eagle swooped down and grabbed something offshore near the island (because of the density of the alder we could not positively identify it). The adult loons immediately started giving 3-note wails and 3-note tremolos, and the male let out several yodels. At 11:00 the eagle attempted to fly with the loon chick (now visible) in its talons, but had trouble becoming airborne in the alder thicket. Thirty seconds later, the eagle attained flight without the chick in its talons and returned to its previous perch in the tamarack. It remained there for 10 min before it flew from the area. The adult loons continued to wail and tremolo for 20 min while swimming around the island. They remained in the area until 12:25, then swam about 300 m to the other side of their territory. We searched for the chick 3 hours later and found it dead, with puncture wounds to the head and a crushed skull. We skinned and mounted the chick as a study specimen, but did not record its body mass.

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Territorial takeover in Common Loons (*Gavia immer*)

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ABSTRACT.—Breeding Common Loons (*Gavia immer*) are well known for vigorously defending their territory from conspecifics. Territory holders are not previously known to be supplanted by loons during the breeding season. I observed a pair of adult Common Loons displace a resident pair from their territory shortly after a territorial conflict; the takeover coincided with the death of the resident loons' chick caused by an adult Bald Eagle (*Haliaeetus leucocephalus*). *Received 27 Feb. 1998, accepted 7 Sept. 1998.*

Common Loons (*Gavia immer*) are philopatric, but territory switching occurs infrequently (Piper et al. 1997; Evers, Reaman, Kaplan, and Paruk, unpubl. data). Our understanding of territory switching in Common Loons remains largely unknown (Piper et al. 1997). In 1995–1997, while coordinating studies of parental effort and social flocking in Common Loons at the Turtle Flambeau Flowage in northern Wisconsin (46° 00′ N, 90° 10′ W), I observed a territory takeover.

The Turtle Flambeau Flowage is a large impoundment (5798 ha) that contains 24–26 loon territories. Territories are generally well delineated by coves or islands, but there are several places where the presence of small islands makes it difficult to distinguish individual territorial boundaries.

On 26 July 1996, at 10:30 CST a pair of unbanded loons entered the territory (Long Island, LI) of an established color-banded pair. All four birds moved behind an island and were out of sight for 2 min. A territorial bird (sex could not be determined because of an obstruction) "surface rushed" one of the intruders driving it onto an island with repeated bill thrusts. At 10:42, the territorial pair was reunited and the intruders were no longer in sight.

At 10:58, an adult Bald Eagle (*Haliaeetus leucocephalus*) killed the resident pairs' 15 day-old chick (Paruk et al. 1999). At this age, loon chicks are still dependent upon adults for food and protection from predators (Dulin 1988, McIntyre 1988). The LI pair remained near the location where the eagle killed the chick until 12:25, at which time they swam to the other side of their territory. I searched the territory for the banded loons from 15:25–16:00, but did not observe them. Instead, I observed two unbanded loons in the territory.

On 27 July, I observed two unbanded, paired adults in the LI territory. The original pair was not observed on 27 July, but on 28 July an assistant spotted them several hundred meters south of their former territory. Throughout the rest of the summer, until 18 August, several observations (n = 9) confirmed that the original territorial pair had been supplanted by two unbanded individuals. The unbanded birds were observed foraging, resting and preening in the LI territory until the end of the observation period on 18 August.

Prior to the takeover, a pair of unbanded

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loons engaged the territorial pair on four consecutive days (22–25 July), with several agonistic encounters. On both 24 and 25 July the LI pair left their chick and engaged in ritualized behavior (jerk diving, facing away) with conspecifics for 20 and 26 min respectively. Whether these were the same individuals that took over the territory is unknown. It seems likely that there was a territorial dispute prior to the death of the LI pair's chick and the subsequent takeover.

Common Loons do not typically abandon their territory after the loss of a chick, although they will often show less aggression towards conspecifics and may wander more frequently than loon pairs with chicks (Evers, pers. comm.; pers. obs.). Thus, it is unlikely that the resident LI pair simply abandoned their territory after the loss of their chick.

In 1997, the former LI pair remained together and occupied a new territory 400 m south of their original territory. Two unbanded loons nested in the former LI territory. Zack and Stutchbury (1992) proposed that nonbreeders are likely to acquire territories they visit frequently and Piper and coworkers (1997) proposed that mid- to late seasonal movements observed in loons may be partly explained by their searching for new or unoccupied territories (reconnaissance hypothesis). The lack of distinct physical barriers separating loon territories and the high number of nonbreeders present on the Turtle Flambeau Flowage (Belant 1989, pers. obs.) may result in higher intrusion rates and more interterritorial interaction, lowering territorial stability (Strong and Bissonette 1988; Belant 1991; Piper et al. 1997; Evers et al., unpubl. data). The timing of the observed supplanting/takeover supports the reconnaissance hypothesis for loon movements during mid- to late summer, and suggests that Common Loons may actively engage in territory acquisition during the breeding season. To what extent this takeover was precipitated by the death of the resident pair's chick remains unknown.

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Courtship Behavior of the Buff-necked Ibis (*Theristicus caudatus*)

Nathan H. Rice

ABSTRACT.—Buff-necked Ibis (*Theristicus caudatus*) courtship displays include "Bill Popping" and grasping twigs, behaviors reported for other species of ibis. *Received 4 Dec. 1997, accepted 20 Aug. 1998.*

The courtship displays of the ibises (Threskiornithidae) are poorly known and little documented, including those of the South American Buff-necked Ibis (*Theristicus caudatus*; del Hoyo et al. 1992, Hancock et al. 1992). Here, I present field observations of apparent courtship displays by this species made at Parque Nacional San Luis (22° 40′ S, 57° 21′ W), depto. Concepción, on 25 October 1996, in the semihumid forest/savanna region of northern Paraguay.

At approximately 09:00 I heard and observed two Buff-necked Ibises at the top of a dead tree, approximately 30 m above the ground making snapping noises with their bills. The presumed male and female would, in turn, grasp dead twigs (2–3 cm diameter) with their bills and release them, never breaking the twigs from the branch. Occasionally, the birds would make low grunts. This continued for about 3 min until the birds abruptly stopped, faced each other, pointed their bills vertically (similar to photo in del Hoyo et al. 1992:480) and gave a loud squawking call. Then they slapped their bills together horizontally, making a sound similar to two hollow pieces of bamboo hitting each other, and flew away together to the northwest.

About 30 min later, approximately 1.5 km northwest of the first site, I heard the same snapping sound and quickly located a pair of ibises, perhaps the same birds, displaying in a similar manner. Again, the behavior lasted about 3 min and ended with the birds slapping their heads together and flying away. On 30 October 1997, a male (testes 18 × 11 mm, KU #88342) and female (ovary 20 × 14 mm, largest ovum 3 × 3 mm, oviduct convoluted 3 mm, specimen deposited in Museo Nacional Historia Natural del Paraguay) were collected that may be the pair I observed earlier. Based on the specimen gonad sizes, the birds were in breeding condition.

The behaviors I observed resemble courtship and breeding displays of other ibises (del Hoyo et al. 1992, Hancock et al. 1992). Unmated male ibises use Bill Popping (Hancock et al. 1992) when soliciting females. This behavior involves the bird snapping its gaped bill shut, occasionally making a popping sound. Some ibis grab a twig and shake it during this behavior. The initial "snapping" noise that I heard may have been a product of Bill Popping by the male. Although the pair I observed never removed twigs from the tree, they did grab sticks during the encounter—a further indication that this was the Bill Popping behavior described in Hancock and coworkers (1992).

Males will also respond to females entering their territories with a ritualized form of Sparring display (Hancock et al. 1992). Sparring behavior consists of one bird, in this case the male, lunging at the other. The female will flee and not fight back. Both of the behavioral series I observed ended with the birds confronting one another (i.e., slapping bills together) and then departing. Perhaps this was a modification of the Sparring behavior described in Hancock et al. (1992).

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Habitat Use by Masked Ducks Along the Gulf Coast of Texas

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ABSTRACT.—We counted 47 Masked Ducks (*Nomonyx dominicus*) in seven flocks during the fall and winter of 1992–1993 on 1009 64.75-ha plots in the Coastal Plains of Texas. Among the three wetland subclasses used by Masked Ducks, bird densities were higher on lacustrine littoral aquatic-bed rooted vascular and lacustrine littoral aquatic-bed floating vascular than palustrine scrub-shrub broad-leaved deciduous wetlands. These wetlands provide important habitat even though they are not the most abundant wetlands in the region. *Received 23 June 1998, accepted 25 Aug. 1998.*

Masked Ducks (*Nomonyx dominicus*) are small, scarce, and reclusive inhabitants of wetlands throughout eastern South America and north into Texas and Florida (Johnsgard and Carbonell 1996, Lockwood 1997, Todd 1997). Little ecological data exist for this species anywhere, but particularly at the northern extent of its range. Appropriate habitat has been subjectively defined as overgrown swamps and marshes, where aquatic plants like water hyacinth (*Eichornia crassipes*) and water lilies (*Nymphaceae* spp.) occur (Johnsgard and Carbonell 1996, Todd 1997). Our objective was to quantify habitat use by Masked Ducks in the Coastal Plains of Texas.

The study area covered 5.5 million ha from Galveston Bay, Texas south to the Rio Grande River (Anderson et al. 1996, 1998). The region is dominated by coastal prairie and sandy plains in the southeast, and rice fields and coastal marsh in the northeast (Anderson et al. 1996). Palustrine and estuarine wetlands (Cowardin et al. 1979) are the most abundant of the wetland systems (Muehl et al. 1994).

We conducted ground based surveys of all wetlands located on 512 quarter-sections (64.75-ha plots) in 1991–1992 and 1009 in 1992–1993 (Anderson et al. 1996, 1998). Surveys for Masked Ducks on wetlands were conducted during September, November, January, and March. Wetlands were classified according to Cowardin and coworkers (1979). Surveys were part of a larger project addressing waterbird habitat use (Anderson 1994, Anderson et al. 1996), waterbird abundance (Anderson et al. 1998), and wetland abundance (Muehl et al. 1994).

We compared densities (no./ha) of Masked Ducks among wetland types on which they occurred using ANOVA and Scheffe's procedure as the mean separation technique with $\alpha = 0.05$ (SAS Institute Inc. 1988). We included in the analysis all wetlands of a type on which Masked Ducks were observed (Anderson et al. 1996). We compared microsite habitat use in wetlands with two-way contingency tables and a *G*-test (Sokal and Rohlf 1995). Count

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periods were considered independent because counts were at least two months apart, wetlands were dynamic (Muehl et al. 1994), and the number of birds varied among count periods (Anderson et al. 1996, 1998). All Masked Duck density data were rank transformed (Conover and Iman 1981, Potvin and Roff 1993) because of the large number of wetlands that had no Masked Ducks. Data were back transformed for presentation.

We did not observe any Masked Ducks during 1991–1992. During 1992–1993, we counted 47 Masked Ducks (September 6; November 4; January 34; March 3) in 7 flocks in 4 separate basins. Masked Ducks occupied 0.3% of quarter-sections surveyed during 1992–1993. All observations were made in the coastal and other crop strata of the area referred to as the Texas Mid-coast (Anderson et al. 1996, 1998). Masked Duck flocks averaged 6.7 birds (SE = 3.16; range 1–25). Sixty-four percent (n = 22) of undisturbed Masked Ducks were observed feeding.

Masked Duck densities (no./ha) on lacustrine littoral aquatic-bed rooted vascular ($\bar{x}$ = 0.93; SE = 0.52) and lacustrine littoral aquatic-bed floating vascular ($\bar{x}$ = 0.40; SE = 0.40) wetlands were not different, but densities on both were greater than densities on palustrine scrub-shrub broad-leaved deciduous ($\bar{x}$ = 0.16; SE = 0.15) wetlands (ANOVA: $F = 10.23$; df = 2, 199; $P < 0.001$). Masked Ducks did not occur on the other 79 wetland subclasses that were surveyed. Masked Ducks were equally likely to occur in open water (43%) and in emergent vegetation microsites within these three wetland types (57%; G-test: $G = 0.2$; $P > 0.05$).

Masked Ducks occupied wetlands that averaged 8.25 ha (SE = 1.94) in area. All wetlands were seasonally or semipermanently flooded with fresh water and had emergent vegetation interspersed with open water [i.e., cover type two (Stewart and Kantrud 1971)]. Rooted vascular vegetation on occupied wetlands was primarily yellow lotus (*Nelumbo lutea*), but yellow waterlily (*Nuphar mexicana*) was also present. Floating vascular wetlands were dominated by water hyacinth. Scrub-shrub vegetation was primarily huisache (*Acacia smallii*) and sesbania (*Sesbania drummondii*).

Although few Masked Ducks were observed, it was apparent that they prefered wetlands with abundant vegetation, particularly aquatic-bed and scrub-shrub wetlands. No Masked Ducks were observed in emergent wetlands, as has often been stated (Johnsgard and Carbonell 1996, Lockwood 1997, Todd 1997). Masked Ducks also are known to occur in flooded rice fields in Venezuela (Gomez-Dallmeier and Cringan 1990), but none were observed in the Texas rice fields we surveyed.

It is interesting to note that Masked Ducks were not found on smaller (palustrine) aquatic-bed wetlands, which are more common than lacustrine littoral aquatic-bed wetlands in the area (Muehl et al. 1994). Their absence from these wetlands may be related to preference for larger (lacustrine) wetlands, which provide greater habitat diversity, increased protection from predators, and more food resources (Anderson et al. 1996). However, Weller (1968) and Todd (1997) indicated that Masked Ducks can use smaller wetlands than other stiff-tailed ducks because they can take-off vertically like dabbling ducks.

Previously, no specific information existed on Masked Duck densities (Johnsgard and Carbonell 1996). Anderson and coworkers (1998) estimated 3817 Masked Ducks occurred in coastal Texas during January 1993, but only 354 during March 1993. Masked Ducks are not as abundant or wide-spread as other waterfowl species in the study area and are rare throughout their range (Johnsgard and Carbonell 1996). The presence of Masked Ducks in Texas may be a temporary phenomenon (Johnsgard and Hagemeyer 1969, Blankenship and Anderson 1993) or they may always be present, but seldom seen, as a result of their rarity, secretive nature, and the preponderance of private property in Texas.

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Gizzard Contents of Piping Plover Chicks in Northern Michigan

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ABSTRACT.—The diet of Piping Plovers (*Charadrius melodus*) is not well known and information on diet requirements will enhance food resource assessment and identification of suitable habitat for this rare species. Discovery of four dead Piping Plover chicks at Grand Marais, Michigan, allowed us to examine their digestive tracts for identifiable prey. Gizzard contents represented 16 families in 6 orders of freshwater and terrestrially occurring insects confirming behavioral observations that plover chicks opportunistically capture insects in shallow water and along shorelines. The most commonly taken orders were Hymenoptera, Coleoptera, and Diptera. *Received 6 May 1998, accepted 30 Aug. 1998.*

Little is known about the diet or foraging behavior of the Piping Plover (*Charadrius melodus*) during any part of its annual cycle. Federal threatened and endangered status (U.S. Fish and Wildlife Service 1985) and sensitivity to human disturbance preclude collection of birds for stomach content analysis and require use of nondisruptive techniques to sample food while plovers are present. Because food availability is critical to shorebird reproductive success, migration, and overwinter survival (Howe 1983, Helmers 1992), assessment of food resources is an important component of conservation efforts for this species. Direct observations of food preference and foraging ecology are needed to im-

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prove assessment of food resources and allow identification of areas appropriate for critical habitat designation and for reintroduction efforts (U.S. Fish and Wildlife Service 1988).

The Piping Plover is a visual rather than tactile feeder, capturing invertebrates moving on the beach surface. Information on diet has been derived from gizzard contents (Bent 1929), direct observation of feeding (Cairns 1977), sampling of organisms present in the habitat (Whyte 1985, Nordstrom 1990, Loegering 1992, Nordstrom and Ryan 1996) and fecal analysis (Nicholls 1989, Shaffer and Laporte 1994); however, studies of prey actually consumed by Piping Plovers have been reported only for marine environments. General diet for the species is described as freshwater and marine invertebrates washed up on the shore and terrestrial invertebrates (Haig 1992). Insects appear to be a major dietary component in most or all habitats occupied by Piping Plovers throughout the year.

While monitoring plover nests in Michigan during 1996 and 1997, we salvaged carcasses of four chicks and examined gizzard contents. We believe this is the first direct information on diet reported for Piping Plovers from the Great Lakes population.

STUDY AREA AND METHODS

In 1996 three pairs of Piping Plovers nested near the mouth of the Sucker River east of Grand Marais, Michigan (46° 40′ N, 85° 56′ W) on the shore of Lake Superior. Two chicks from one of these pairs disappeared at six days of age. The carcass of one was discovered approximately 1.5 weeks later and the other 2.5 weeks later. The fresh carcass of the third chick from this brood was discovered a few hours after its disappearance at 19 days of age. In 1997, a fourth Piping Plover chick carcass was found in the same general area. This chick disappeared from its brood when it was one week old and was found three days later. The digestive tract from each chick was removed, cut open and flushed with 70% ethyl alcohol. Only gizzards yielded identifiable samples. The contents of the four gizzards were examined with a dissecting microscope and identified to family by an entomologist (Scholtens) familiar with insects of the region. Numbers of individual prey were estimated.

RESULTS AND DISCUSSION

Parts of adult and larval insects were the only prey identified in the gizzards. Prey represented 16 families in 6 orders: Hymenoptera (32%), Coleoptera (29%), Diptera (28%), Hemiptera and Homoptera (10%), and Ephemeroptera (1%). Based on the natural history of these families in northern Michigan, they can be characterized as inhabiting shoreline/wet sand (Dolichopodidae, Ephydridae), shallow water/wet sand (Corixidae, Dytiscidae, Haliplidae), beach vegetation/sand surface (Aphididae, Braconidae, Carabidae, Cicadellidae, Curculionidae, Ichneumonidae) and general shoreline habitat (Superfamily Chalcidoidea, Chironomidae, Formicidae, Muscidae, unidentified Ephemeropteran family). The only previous information related to the prey of the Great Lakes Piping Plover was found in a study of invertebrates present within National Park lands being assessed as potential reintroduction sites (Nordstrom 1990, Nordstrom and Ryan 1996). Nordstrom (1990) found 48 families of 9 orders of insects and 1 family of arachnid on the shore of Lake Superior in Pictured Rocks National Lakeshore (approximately 20 km west).

In the Great Lakes region, Piping Plovers nest on wide sandy beaches and forage along the water line of Lake Michigan and Lake Superior. Birds occasionally glean insects from beach vegetation and at some sites forage along the edges of creeks and shallow beach ponds. At the Grand Marais site, adults and chicks were observed foraging primarily along the edge of the Sucker River and in shallow pools of water and wet depressions in the sand along the river. Aquatic insects in the chick gizzards are consistent with this observation, and the presence of terrestrial, phytophagous insects indicates that chicks also gleaned insects from beach vegetation. Presence of aquatic algae-eating beetles (Haliplidae) in the gizzards suggests that chicks picked insects from algae on the river edges. While Nordstrom and Ryan (1996) reported a predominance of Dipterans in the Lake Superior habitat they sampled, we found predominantly Hymenopterans and Coleopterans in the chick gizzards. We identified two families (Corixidae and Dytiscidae) in the gizzards that were not reported by Nordstrom (1990). Members of both families inhabit streams, ponds, and stagnant pools associated with beaches.

Given the constraints on disturbance and collecting, opportunistic discovery of dead plovers and subsequent study of their diges-

tive tracts may contribute information vital to understanding the diet of this endangered species. For example, insects gleaned from vegetation, algal mats, and the water surface probably would not be revealed by traditional methods (e.g., sticky traps) used to sample invertebrates in the habitat. The information on foraging behavior and prey selection that both gizzard and fecal analyses provide is needed to increase accuracy of methods used to sample invertebrates from the habitat. It is important to note that all three methods of quantifying plover food resources (gizzard analysis, fecal analysis, and sampling from habitat) may be greatly affected by the time samples are obtained because of temporal variation in insect abundance. Fecal analysis offers the advantage that numerous samples can be collected from the same individuals to reveal temporal patterns of prey selection; however, this method underestimates soft-bodied invertebrates (Shaffer and Laporte 1994). Because gizzard contents have undergone less digestion, they are presumably less biased in this regard, but this has not been confirmed.

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Nesting of Four Poorly-Known Bird Species on the Caribbean Slope of Costa Rica

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ABSTRACT.—We describe the nests of four species of birds from the Caribbean slope of Costa Rica. A Great Potoo (*Nyctibius grandis*, nest previously unknown from Mesoamerica) nest was nothing more than a crevice in a high branch of a large tree, similar to those reported in South America. A nest of the Torrent Tyrannulet (*Serpophaga cinerea*) was found along a river at 35 m elevation, much lower than previous breeding reports for this normally montane species. Also, we confirm systematists' predictions that the Tawny-chested Flycatcher (*Aphanotriccus capitalis*), a species of near-threatened conservation status, is a secondary cavity nester. Finally, we report on the second known nest of the Sooty-faced Finch (*Lysurus crassirostris*) from montane forest. *Received 20 May 1998, accepted 7 Oct. 1998.*

RESUMEN.—Describimos los nidos de cuatro especies de aves de la vertiente del caribe en Costa Rica. Un nido de *Nyctibius grandis* (nido era anteriormente desconocido en Mesoamerica) era nada más que una grieta en una rama alta de un árbol grande, muy parecido a los nidos de la misma especie encontrados en América del Sur. Describimos un nido de *Serpophaga cinerea*, el cual fue encontrado en un río a los 35 msnm, mucho más bajo que los otros registros de esta especie del bosque montano. Describimos unas observaciones que indican que el *Aphanotriccus capitalis*, una especie ligeramente amenazada desde la punta de vista conservacionista, anida secondariamente en los huecos dentro de los arboles. Finalmente, presentamos la segunda descripción del nido de *Lysurus crassirostris*, el cual fue encontrado en un bosque montano.

Despite decades of intensive ornithological study, the nests and eggs of a number of Central American bird species are poorly known (Skutch 1954, 1960; Stiles and Skutch 1989). Especially enigmatic are species inhabiting the relatively inaccessible habitats of the humid Caribbean slope. The lack of reproductive information about these species hinders phylogenetic studies of the relationships among avian lineages, studies of intraspecific variation, general analyses of reproductive behavior, and the development of management practices for conserving avian biodiversity. Here we describe the first Mesoamerican nest of the Great Potoo (*Nyctibius grandis*), the first lowland nest of the Torrent Tyrannulet (*Serpophaga cinerea*), the first nest of the Tawny-chested Flycatcher (*Aphanotriccus capitalis*), and the second nest of the Sooty-faced Finch (*Lysurus crassirostris*).

STUDY AREA

Our observations were made in the 45,000 ha La Selva-Braulio Carrillo National Park reserve complex in Heredia Province, northeastern Costa Rica. The reserve complex, the largest protected elevational transect in Central America, extends from montane rain forest surrounding the Barva Volcano at 2,900 m down to lowland wet forest at the La Selva Biological Station at 35 m elevation on the Caribbean slope (Timm et al. 1989).

Observations were made in 1997 during routine bird monitoring activities at La Selva (10° 26′ N, 83° 59′ W) and at a remote campsite at 1070 m elevation in Braulio Carrillo National Park (10° 16′ N, 84° 5′ W). Annual rainfall at La Selva averages 3962 mm, with a relative dry period between January and March during most years (Sanford et al. 1994). Although precipitation data are scarce for higher elevations, annual rainfall may average over 5000 mm at the 1070-m site, where clouds frequently bathe the premontane rain forest in mist (Hartshorn and Peralta 1988). Average canopy height varies from 28–38 m at La Selva to 22–36 m at 1070 m (Lieberman et al. 1996).

NEST DESCRIPTIONS AND DISCUSSION

Nyctibius grandis.—The Great Potoo is one of three Central American species of the genus *Nyctibius*, the only genus in the exclusively Neotropical family Nyctibiidae. Although difficult to observe in daylight because it roosts motionless on canopy branches, the

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FIG. 1. Adult and nestling Great Potoo (*Nyctibius grandis*) on the branch of a large *Hernandia didymantha* tree, La Selva Biological Station, Costa Rica, April 1997.

Great Potoo is readily detectable at night by its characteristic calls (Perry 1979, Slud 1979). It ranges from southern Mexico to southeastern Brazil and central Bolivia (AOU 1998, Howell and Webb 1995).

On 5 February, a visitor to the station (K. McGowan) found a single Great Potoo perched 34 m high on the branch of a 44 m tall *Hernandia didymantha* (Hernandiaceae) tree. The tree was located 500 m inside of old growth forest, at the edge of a large treefall gap on a steep hill. The bird was perched on an upward sloping section of an S-shaped branch approximately 20 cm in diameter. Thereafter on daily visits, we observed a bird in exactly the same position.

On 4 April, we observed for the first time a fully feathered chick on the branch in front of the adult. The chick was paler in coloration than the adult and about one quarter the size (Fig. 1). On subsequent days, the chick moved between a hidden position under the adult's breast feathers and the branch immediately in front of the adult. The adult remained almost motionless and never moved along the branch. We last saw the birds on 20 April. Despite extensive searches on all neighboring branches in the following days and months, neither adult nor young was seen again.

The motionless adult we saw was probably incubating an egg initially and then brooding a chick, although we could not determine the hatching date. Although collections of adults on eggs in Brazil and observations of *N. griseus* in Costa Rica indicate that males incubate during the day (Skutch 1970, Sick 1993), we could not identify the sex of the individual (or individuals) we saw because sexes are similar in outward appearance in Great Potoos (Land and Schultz 1963, Wetmore 1968). No nest was visible and, from our vantagepoint 30 m from the tree and level with the nest, only a slight crevice in the branch was visible. Although the location appeared precarious, reports from Brazil suggest that a notch in the nest branch can securely hold an egg (Sick 1993).

At a nest in Venezuela, a chick remained with its parent for a month, and then alone for almost another month before growing to a size greater than two-thirds that of the adult and dispersing (Vanderwerf 1988). This observation suggests that the chick we observed, which never attained half the size of the adult, did not survive. In addition, the wings did not appear sufficiently developed for sustained flight. Despite an extensive ground search, we found no evidence of its having fallen from the nest. The chick may have been taken by an arboreal predator such as a monkey (*Cebus capucinus, Ateles geoffroyi,* or *Alouatta palliata*), tayra (*Eira barbara*), or Collared Forest-Falcon (*Micrastur semitorquatus*), all common in the area. Even though the attempt was probably unsuccessful, its daily survivorship rate in the (presumed) egg and chick stage of 98.7% is substantially higher than the 93% rate measured for understory cup-nesting birds the same year in the same area (B. Young, unpubl. data).

Serpophaga cinerea.—The Torrent Tyrannulet is a conspicuous resident of highland rivers from Costa Rica to Venezuela and Bolivia (AOU 1998). Their cup-shaped nest attached to vegetation above rivers is well known (Skutch 1960). The elevational distribution of the species is variously described as 250–2500 m in different parts of its range (Meyer de Schauensee and Phelps 1978, Hilty and Brown 1986, Stiles and Skutch 1989, Ridgely and Gwynne 1993, Ridgely and Tudor 1994).

We first detected Torrent Tyrannulets on the

Sarapiquí River in 1994 in Chilamate, 5 km west of La Selva at an elevation of 40 m. In March 1997, we began seeing individuals along the same river where it passes through La Selva at 35 m elevation. These were the first observations of the species in La Selva in four decades of ornithological investigation (Levey and Stiles 1994). During the first week of April, a pair of tyrannulets began construction of a nest 0.5 m above the water level in shrub vegetation growing in the middle of a small island in the river, which is approximately 80 m wide and 1 m deep at this point. The nest was typical for the species in being cup shaped, supported by vertical branches, with feathers and moss woven into the structure (Skutch 1960). We monitored the nest every 2–5 days until 22 April when two eggs were found in the nest. During each visit, two birds were active near the nest, adding material and adjusting its structure. On our next visit, on 30 April, the nest had disappeared and the birds were not present.

Despite its conspicuousness on rivers, previous reports of the species occurring in the lowlands are of scattered observations of individuals as low as 100 m elevation (Hilty and Brown 1986, Ridgely and Gwynne 1993, Ridgely and Tudor 1994). The Torrent Tyrannulets we observed may have strayed from their higher elevation habitat because of a hydroelectric project in progress higher up the Sarapiquí River.

Aphanotriccus capitalis.—The Tawny-chested Flycatcher occurs in second growth and disturbed forest in Nicaragua and Costa Rica (AOU 1998). Nests of both this species and its congener are apparently undescribed (Lanyon and Lanyon 1986), and both have near threatened conservation status as a result of their small, fragmented ranges (Collar et al. 1994). We provide two observations to suggest the species nests in either cavities or crevices in trees.

On 23 April, a group of birdwatchers spotted a pair of Tawny-chested Flycatchers building a nest in the hollow of a dead branch stub in an otherwise live *Alchornea costaricense* (Euphorbiaceae) tree. On 30 April, we again observed two birds carrying fine nesting material, including moss, to the hollow for about 30 min. The birds apparently abandoned the attempt, as we never saw them there again. The rectangular hollow was oriented slightly upward, 8 cm deep and 25 × 8 cm wide, 1.5 m up in the 36 cm dbh tree. The tree was in a small, shady clearing 10 m away from a small (0.25 ha) patch of second growth forest.

A local naturalist guide, E. Castro, reported finding an active nest of this species in a hollow section of a 30 m diameter clump of Asian bamboo (*Guadua* sp.) in a patch of second growth forest 2 km north of La Selva. Castro reported seeing adults carrying food to the nest and later feeding a fledgling in the vicinity. The nest was 5.9 m above the ground, 13 cm in diameter (the diameter of the bamboo), and entered through a 5 cm high by 2 cm wide teardrop-shaped opening. The bottom of the opening was 3 cm above a node, leaving a shallow area for the nest. This finding confirms predictions that *Aphanotriccus* builds nests in crevices based on its phylogenetic closeness to *Lathrotriccus* and *Cnemotriccus,* two genera known to build nests in crevices (Lanyon 1986, Lanyon and Lanyon 1986). This crevice nesting habit may aid in the conservation of the species; *Guadua* bamboo is widely introduced in the region for use in supporting banana trees on plantations.

Lysurus crassirostris.—The Sooty-faced Finch occurs in dense vegetation in wet, mid-elevation forest in Costa Rica and Panama (AOU 1998). Its one congener, the Olive Finch (*L. castaneiceps*), occurs in humid montane forests along the coastal Andes mountains from Colombia to Peru (Ridgely and Tudor 1989).

On 7 May we discovered two adult Sooty-faced Finches entering and exiting a nest 2.1 m high attached to the side of a large *Sommera* sp. (Rubiaceae) tree (dbh = 46 cm) next to our camp at 1070 m, several kilometers inside undisturbed forest. The nest tree was located at the side of a little used trail at the edge of a stream crossing. The nest itself was woven into a thick epiphyte mat on a section of the trunk directly above the 3 m wide stream. The nest was a bulky, covered dome with a side entrance. The nest was almost entirely constructed of fresh moss with a lining of thin, black, stringy fungal rhizomorphs and strips of dried bamboo (*Chusquea* sp.) leaves. The trunk of the nest tree was covered with the same moss as was used to construct the

nest, causing the nest to be fairly inconspicuous.

On 11 May, after observing the adults spending long periods of time in the nest, we examined the eggs. The two eggs were whitish and speckled with lavender. The speckles were densest around the thick ends of the eggs. Assuming the adults were incubating and that the female had finished laying, the clutch size for this nest was two, typical for birds of humid tropical forests (Skutch 1985).

This nest was very similar to the one other nest described for the species, although the latter was built into the side of a fern stem and apparently was not associated with water (Barrantes 1994). These two nests were similar to the single nest of the congeneric Olive Finch described from Ecuador (Schulenberg and Gill 1987). All nests of the two species were bulky and dome-shaped, constructed primarily of mosses on the outside, cryptically situated in moss-dominated vegetation, and, in two cases, located over moving water. The nests of the two species differ in that the Olive Finch nest was built on the side of a rock instead of a tree and had a lining of dry leaves instead of rhizomorphs. The eggs differ substantially in that the eggs of the Olive Finch were immaculate white (Schulenberg and Gill 1987) compared with the spotted eggs found in both Sooty-faced Finch nests (Barrantes 1994). Interestingly, eggs in two collections attributed to the Olive Finch are spotted (Schulenberg and Gill 1987), suggesting that the Ecuadorian discovery of all white eggs may have been atypical for the group.

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Sexual Dimorphism in the Song of Sumichrast's Wren

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ABSTRACT.—We report on a song-like vocalization of female Sumichrast's Wren (*Hylorchilus sumichrasti*). The female song is a series of similar syllables, all at the same low pitch, that varies in length. Thus, it differs strongly from the rich and complex songs of male Sumichrast's Wrens and of most other wrens. *Received 27 Feb. 1998, accepted 25 Aug. 1998.*

There is increasing evidence that female song is not as rare in birds as previously thought (Langmore 1998). Among most wrens, females have songs that are similar to and sometimes combine with those of their mates in antiphonal duets (Skutch 1940, 1960). Until recently, the only reported case of strong sexual difference in wren songs was in the southern House Wren (*Troglodytes aedon*) among which the females give a simple twittering and/or a short trill, at least in Costa Rica and Panama, generally countersinging with the males (Chapman 1929; Skutch 1940, 1953). Distinct female songs have more recently been recorded in other *Troglodytes* wrens—one population of northern House Wren (Johnson and Kermott 1990) and Socorro Wren (*T. sissonii*; Howell and Webb 1995). During fieldwork on the life-history of Sumichrast's Wren (*Hylorchilus sumichrasti*) in Cerro de Oro, Oaxaca (18° 02′ N, 96° 15′ W; Pérez-Villafaña 1997), we recorded the previously unknown song of a female *H. sumichrasti*.

Sumichrast's Wren is sexually monomorphic in plumage. The birds we observed were not color-banded; however, during direct observation of the members of a single pair from March to July 1994, we realized that the previously unrecorded song was always made by the bird that did not emit the more complex song described by Howell and Webb (1995) and Gómez de Silva (1997). By analogy with other wrens that have strong sexual differences in song (in which the female's song is the simpler one), and from the birds' behaviors, we concluded that this previously unrecorded song was the song of the female. We subsequently have heard this "female song" at different points along a 738 m transect at Cerro de Oro, and throughout the range of Sumichrast's Wren: 2 km south of Amatlán (18° 50′

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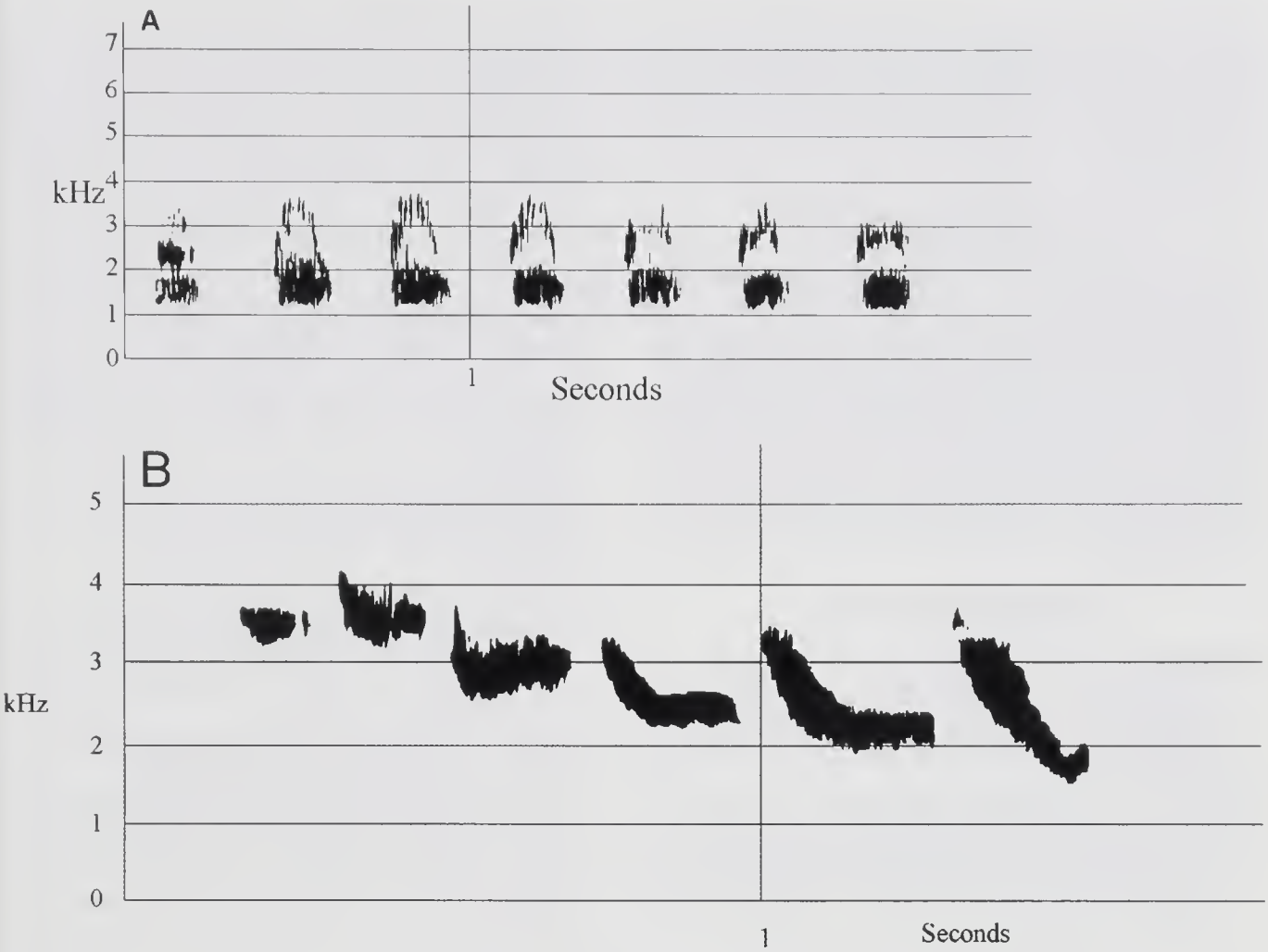

FIG. 1. Songs of female (A) and male (B) Sumichrast's Wren (*Hylorchilus sumichrasti*). Recorded by S. N. G. Howell 2 km south of Amatlán, Veracruz.

N, 96° 55′ W), Agua Escondida (18° 32′ N, 96° 47′ W), Oaxaca/Veracruz border on the road to San Juan del Río (17° 32′ N, 95° 44′ W), and 2 km south of Bethania (17° 56′ N, 96° 01′ W).

The distinction between songs and calls is sometimes unclear. In general, calls comprise one or two syllables whereas songs are longer vocalizations comprising multiple syllables (Langmore 1998). The "female song" of Sumichrast's Wren is a simple phrase consisting of a single repeated syllable (fundamental < 2 kHz). In this respect, it resembles the main song of the Cactus Wren (*Campylorhynchus brunneicapillus*) rather than the rich and complex songs of male Sumichrast's and of most other wrens. The female song had 4–22 such syllables per song. The pause between the first and second syllables, and to a lesser extent the pause before the last syllable, are the longest. This simple song of uniform frequency contrasts with the males' complex songs which spans a range of frequencies and contains syllables of variable form (Fig. 1, see also other sonograms of male songs in Gómez de Silva 1997 and Atkinson et al. 1993).

Females sing less frequently than males. Along the transect at Cerro de Oro, censused twice a month between April 1994 and March 1995, only 28.5–75% as many females were recorded singing per morning as males. Females sometimes countersang or sang at the same time as males. In the one focal pair, the female countersang with the male 46.2% of the time. Females usually sang with their bodies held upright and their tails pointing downward, the same position as singing males in Cerro de Oro.

Nonantiphonal female songs may be more widespread in wrens than previously thought. The few records may be due to a scarcity of detailed observation. Carmona (1989) observed that female Canyon Wrens (*Catherpes mexicanus*) produce a vocalization that is dif-

ferent from the male's but gave no details about the vocalization. A systematic survey of female songs (or their general absence) in wrens appears to be an interesting possibility for research.

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An Incident of Female-Female Aggression in the House Wren

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ABSTRACT.—In this paper we describe one example of female-female aggression in the House Wren (*Troglodytes aedon*). An intruding female usurped the resident female and paired with the resident male. House Wrens are known for committing infanticide as well as puncturing and removing eggs of conspecifics and other species. These behaviors have been mainly attributed to resident and floating males, but we suggest that females may also be responsible. *Received 22 July 1998, accepted 3 Nov. 1998.*

In many passerine bird species, males establish breeding territories in the spring, which they defend against intruders. This form of sexual competition among males has been recognized as one of the driving forces behind mating patterns and parental care (Davies 1991, Andersson 1994). Aggression among females has received much less attention, although it has recently been shown to be more common among birds than initially assumed (Lenington 1980, Leffelaar and Robertson 1985, Searcy 1986, Martin et al. 1990, Slagsvold 1993, Hansson et al. 1997, Liker

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and Székely 1997). Female-female aggression may affect several aspects of mating systems and parental care, for example, maintaining monogamy (Slagsvold 1993) or reducing harem size (Hurly and Robertson 1985). Female-female aggression in Red-winged Blackbirds (*Agelaius phoeniceus*; Beletsky 1996) as well as Lapwings (*Vanellus vanellus*; Liker and Székely 1997) is strongest early in the breeding season when females first settle on the territories. One evolutionary force behind female-female aggression in polygynous mating systems is the conflict between females for the male's parental investment (Slagsvold and Lifjeld 1994). However, female-female aggression is not limited to polygynous mating systems (Slagsvold 1993). Here we report an incident of female-female aggression in the House Wren (*Troglodytes aedon*).

We have been studying a population of House Wrens on the E. N. Huyck Preserve and Biological Research Station in Rensselaerville, New York since 1992 and have color banded all individuals since 1995. On 17 May 1997, 07:15 EST we observed a fight between two females that lasted for 30 minutes. Female A, who had been paired to the resident male of the territory since 12 May was chased in circles both in the air and on the ground by female B. Female B had been the resident female of the same territory in 1996 but was paired with a different male. The 1996 male was not seen in 1997. The fight included chases by female B with occasional aggressive interactions that included bodily contact and pecking. Neither female vocalized during the encounter. The resident male was perched and visible during the whole fight; he sang but did not participate in the fight. Female B eventually usurped the territory from female A, paired with the resident male, and took over the nest that was close to completion. Female A was not seen again during the 1997 breeding season. We suggest that female B was probably fighting for the territory rather than for the resident male. One of the most successful males in our study population, who was polygynous in 1996 and 1997, occupied the adjacent territory and was at that time unpaired. Female B did not pair with this unmated male but returned to the territory with which she was familiar.

Many researchers strongly suspect that resident birds and probably non-resident floaters as well (Johnson and Kermott 1993) routinely enter territories not their own and kill and/or remove eggs or young from nests (Belles-Isles and Picman 1986, 1987; Quinn and Holroyd 1989; Kermott et al. 1991). Until recently these birds have been assumed to be male (Quinn and Holroyd 1989, Kermott et al. 1991), but it now appears that residents need to be concerned about intruding females as well. This and other observations of female-female aggression (Freed 1986, Johnson and Searcy 1996) demonstrate that female House Wrens may play an equally important role as the males in the selection of nest sites, territorial defense, and intraspecific aggression.

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Nest Reuse by Wood Thrushes and Rose-breasted Grosbeaks

Lyle E. Friesen,[1,2] Valerie E. Wyatt,[1] and Michael D. Cadman[1]

ABSTRACT.—We report on two instances of nest reuse by Wood Thrushes (*Hylocichla mustelina*) within the same breeding season, and three cases of nest reuse in successive years, two by Wood Thrushes and one by Rose-breasted Grosbeaks (*Pheucticus ludovicianus*). In each of the five cases of nest reuse, host young were successfully fledged in the original nesting episode and in the second nesting episode. Although occasional nest reuse within a single breeding season has been reported before, our study is the first to document reuse of the same nest in successive years by Wood Thrushes and Rose-breasted Grosbeaks. *Received 29 April 1998, accepted 4 Oct. 1998.*

Open nesting passerines, with the possible exception of tyrannid flycatchers (Curson et al. 1996), seldom reuse nests within and between breeding seasons (Briskie and Sealy 1988). Earlier authorities (Weaver 1949, Brackbill 1958) were unaware of nest reuse by Wood Thrushes (*Hylocichla mustelina*). Roth and coworkers (1996) documented occasional nest reuse by Wood Thrushes during the same breeding season (three cases out of 389 first nests). However, they did not report any nest reuse between years, describing such an event as unlikely because nests usually disintegrate after the nesting season. We report on two cases of nest reuse by Wood Thrushes within a breeding season and three cases of nest reuse in successive years, two by Wood Thrushes and one by Rose-breasted Grosbeaks (*Pheucticus ludovicianus*).

Data presented in this study were gathered in the course of a larger study of the nesting success of Wood Thrushes and Rose-breasted Grosbeaks conducted in 1996 and 1997 in Waterloo Region, a fragmented agricultural landscape located in southwestern Ontario (see Friesen et al., in press for a description of the landscape). In these two years, 154 Wood Thrush nests and 63 Rose-breasted Grosbeak nests were found and regularly monitored to determine their outcome.

Two Wood Thrush nests (one each year) were reused during the same breeding season, with young successfully fledging in all four nesting attempts (see Wyatt 1997 for a de-

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tailed account of one of the renests). Neither of these nesting attempts were parasitized by Brown-headed Cowbirds (*Molothrus ater*) although 47% of Wood Thrush nests on our study sites contained cowbird eggs or young (Friesen et al., in press). In 1996, 20 days elapsed between the fledging of the first brood and the initiation of the second clutch (June 20 to July 10); in 1997, this interval was 13 days (June 25 to July 8). Neither of the original nests appeared to have been relined or refurbished prior to its second use. It is likely that the same pairs reused each of the nests but this could not be confirmed because the birds were not color-banded. Studies of banded birds in Waterloo Region in 1998 showed that at least half of the pairs attempted two broods in a nesting season (Friesen, unpubl. data).

We mapped and marked all of the Wood Thrush nests found in 1996 (n = 61) and observed, through visits to the sites the following spring prior to the breeding season, that five (8%) of them survived the winter seemingly intact. Two of these nests were subsequently reused in 1997: one nest which fledged three Wood Thrushes and one cowbird in 1996, fledged four thrushes and two cowbirds the following year; the other nest fledged two thrushes and one cowbird in each of the years. Neither nest appeared to have been significantly renovated in the second year, although both were in poor repair by the time the young fledged in 1997.

Rose-breasted Grosbeaks are typically single brooded in southern Ontario (Friesen et al., in press) and we found no evidence of nest reuse within the same breeding season. Three (12%) of the 24 grosbeak nests we found in 1996 survived the winter. One of these, in which three young were fledged in 1996, was reused in 1997 and again fledged three young.

Our results suggest that nest reuse is a consistent, albeit infrequent, breeding strategy. The reuse of old nests may have resulted from a shortage of suitable nesting sites although it seemed to us that apparently suitable alternative sites were present nearby. It may also be that the birds reusing nests recognized the latter as being of high quality, borne out by the fact that all five nest reuses resulted in fledged host young. Our study is a reminder to researchers of the importance of monitoring the status of used nests both within and between breeding seasons.

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Singing in a Mated Female Wilson's Warbler

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ABSTRACT.—A female Wilson's Warbler, *Wilsonia pusilla*, was heard singing regularly on the territory of a male in middle inner-coastal California during early April, 1996, and occasionally after mid-April. Based on their behavior, the resident male and the singing female were paired. The female averaged about four songs/min during singing bouts, and was heard about 30% of the time during early April. The female's song was high pitched, and did not resemble typical male "chatter" song. In contrast to the functions of female song in many tropical and some temperate parulids, this song seemed to serve as a simple contact vocalization between mates, as call notes might. A single female song heard in a newly formed pair in 1997 raises the possibility that such songs might function in pair formation. *Received 10 April 1998, accepted 25 Aug. 1998.*

Singing by female birds, while common and perhaps characteristic among tropical species, occurs much less commonly among temperate species (Morton 1996). Tropical and temperate wood warblers follow this pattern. Songs of tropical parulid females commonly are used in "duets" with mates and may function in pair formation, communication with mate, and territorial defense (Spector 1992). To serve such functions, consistency in occurrence and stereotypy in form of song seem to be required. Song in temperate parulid females, where reported, has typically occurred in few females within a population, and in some cases song patterns have varied among females (e.g., Nolan 1978, Hobson and Sealy 1990). This suggests that song in temperate parulid females is idiosyncratic, and/or serves very limited and infrequent functions. To our knowledge, female song has been reported in ten temperate parulid species from six genera: *Vermivora, Parula, Dendroica, Setophaga, Seiurus,* and *Geothlypis* (Spector 1992, Moldenhauer and Regelski 1996). Here we report singing in a mated female Wilson's Warbler, *Wilsonia pusilla.*

We first heard the female song on 3 April, 1996, from the territory (ca 0.2 ha) of a color-banded resident male (the "male") Wilson's Warbler in the Nature Study Area of Tilden Regional Park, Contra Costa Co., California. We subsequently heard this unusual (compared with typical male "chatter" song; Fig. 1B) and distinctive song at various times between 07:15 and 11:40 PST through 18 April. The high frequency song sounded "sharp" and "squeaky" (Fig. 1A, C). It was delivered at a rate of 4.0 ± 0.6 songs/min (range = 2–6, n = 7) within singing bouts (we considered a singing bout to be continuous singing with no pause greater than one minute between songs). On four separate occasions, we observed the beak of a Wilson's Warbler to open and move as the female song was heard, confirming that the song came from the species. Behavioral observations (see below) indicate that the singer was the resident female (the "female") in the territory she occupied. This female also frequently chipped within this territory (Fig. 1C).

From 3 through 12 April we located the female during 30% of our observation time (490 min) based on hearing her song and/or sighting the singing bird. We confirmed that the male was in her proximity 20% of our observation time (the male usually did not sing and often was more difficult to locate). Bouts of female song that we monitored lasted 11.5 ± 3.0 min (range = 1.5–27, n = 11), and male-female separation distance was 6.8 ± 1.2 m (range = 2–20, n = 22). From 13 through 30 April, we located the female just 5% of our observations time (825 min), and located the male in her proximity only 2% of that time. Bouts of female song that we monitored lasted 3.1 ± 1.3 min (range = 1.5–7.0, n = 4), and mean male-female separation distance was 4.4 ± 1.2 m (range = 0–12, n = 11). Three consecutive singing bouts monitored on 18 April

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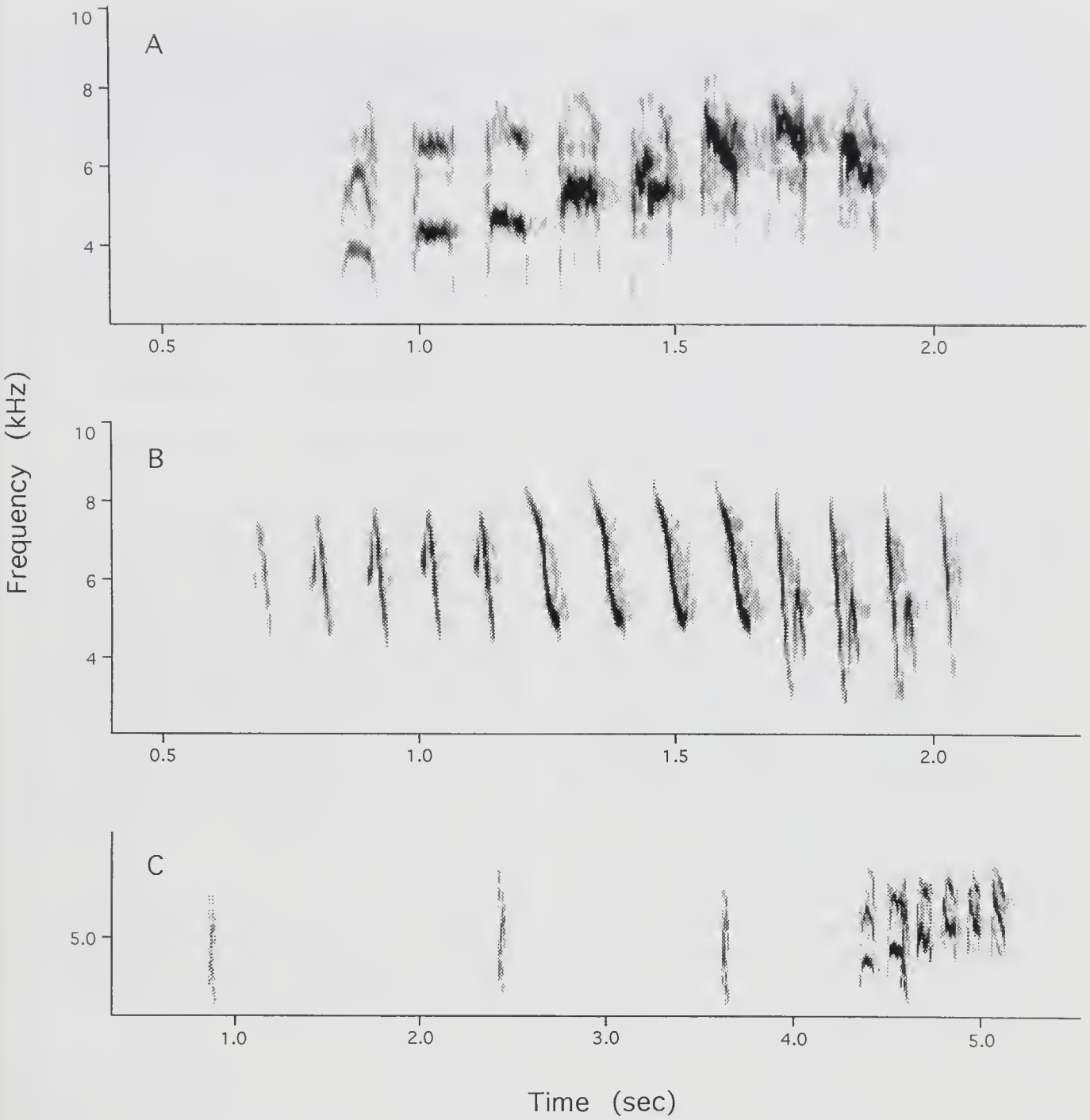

FIG. 1. Wilson's Warblers vocalizations recorded in April, 1996, within a breeding territory at a study site in Contra Costa Co., California. A. Eight-note song, sung by resident female, with resident male in close proximity. B. A typical "chatter song" of resident male. C. Three call notes, followed by a 6-note song, by resident female. Recordings made by W. M. Gilbert using a SONY TCD-D8 recorder and a Sennheiser K3U microphone. Spectrograms made with Canary 1.2.1 software (Cornell Laboratory of Ornithology) using a Macintosh 7.5 system computer.

had separation intervals of 30 and 44 min. At no time during our observations did we notice unusual resident male behavior (compared with other mated males) that might have elicited singing in the female.

We relied on several contextual clues to determine the sex of the bird singing the unusual song (the sexes of west coast Wilson's Warblers often are indistinguishable in the field), and that bird's relationship to the resident male on whose territory it sang: (1) the male was mated (although we found no direct evidence of breeding, unpaired males tend to sing persistently, often from exposed perches, while this male sang sporadically, often from undergrowth); (2) we consistently heard the

unusual song from within the male's territory, but not from beyond its borders; (3) about two-thirds of the time that we heard the unusual song, the male was sighted within 25 m of the singer, and the male and the singer often foraged in the same tree, in adjacent trees, or in the same restricted area of undergrowth; (4) even though the two birds frequently were close, they never were in conflict; (5) we never simultaneously sighted nor heard the two birds at opposite ends of the territory; and (6) we never consistently sighted a third Wilson's Warbler within the male's territory, as we would have had the male been mated to a bird other than the one singing the unusual song. Based on this evidence, we concluded that the bird singing the unusual song was a female mated with the resident male on the territory where she sang.

On 27 March, 1997, WMG observed a newly formed (<3 h) pair of Wilson's Warblers on a territory adjacent to that in which we heard the female song in 1996. The new pair was in view for 41 min and the color-banded male followed the unbanded female through vegetation ranging from undergrowth to tree canopy. Amid continuous chipping from the pair, WMG heard one song indistinguishable by ear from the female songs heard in 1996. It could not be determined which bird delivered the song, nor if the female of the pair was the same bird that sang the female songs in 1996.

Information on female song in temperate parulid species is limited. In female Prairie Warblers (*Dendroica discolor*), a limited number of females' songs heard were all simple and perhaps "primitive," highly variable among individuals, and unlike normal male songs (although some were identifiable to species). These songs were delivered early in the season, were heard sporadically, and may have been delivered by older females displaying more male-like behavior (Nolan 1978). In Yellow Warblers (*Dendroica petechia*), Hobson and Sealy (1990) suggest that female song can function in intrasexual conflicts within very dense breeding populations.

The singing we heard from a female Wilson's Warbler(s) occurred early in the season and possibly came from an older bird(s), as would be consistent with some findings of Nolan (1978) for the Prairie Warbler and with some correlates of female song in other species where usually only the male sings (Nice 1943). Other aspects of the singing we heard appear to differ from what occurs in females of some other parulids, however. The songs we heard were not used in duets with mates, as in many tropical species (Spector 1992). There was no evidence that they functioned in intrasexual conflicts within dense populations (Hobson and Sealy 1990). Finally, we heard the female consistently for more than a week in early April, 1996, as opposed to isolated bouts of singing heard on single days (Nolan 1978).

The female songs we heard in 1996 (as well as the single song heard in 1997) were interspersed between chip notes and usually delivered with the resident male close to the female. This suggests the songs may have functioned to communicate with a mate. The single song heard in 1997 (if delivered by a female and one different from the singer of 1996) introduces the additional possibility that the song could serve a special communicatory function during early Wilson's Warbler pairing. If so, then the persistent female singing heard in 1996 would have been an abnormal carry-over of that behavior into the nesting period. Singing in that female may have reflected an abnormal hormonal balance, similar to effects of testosterone injection in stimulating song in female birds that normally don't sing (e.g., Baptista and Morton 1988).

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Laying Time of the Bronzed Cowbird

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ABSTRACT.—We report the first observations of egg laying by the parasitic Bronzed Cowbird (*Molothrus aeneus*). Three direct observations and two estimates of laying times were made at two Northern Cardinal (*Cardinalis cardinalis*) nests. Bronzed Cowbirds laid at 18.2 min ± 1.7 (SE) before sunrise (range 14–24 min). Laying lasted 5–10 seconds. Although the parasitic Brown-headed Cowbird (*M. ater*) and sometimes Shiny Cowbirds (*M. bonariensis*) also lay before sunrise, direct observations of laying by other cowbirds are required before it can be concluded that pre-sunrise laying is an adaptation for brood parasitism. *Received 9 June 1998, accepted 5 Sept. 1998.*

Avian brood parasites that are surreptitious when parasitizing nests may avoid detection by their hosts. Indeed, they often lay their eggs in a matter of seconds; Sealy and coworkers (1995) found this behavior to be unique to the diverse groups of brood parasites. The parasitic Brown-headed Cowbird (*Molothrus ater*) generally lays in the minutes prior to sunrise and it has been suggested that laying at this time, presumably when hosts are less likely to be at their nests, is an adaptation for brood parasitism (Chance and Hann 1942). Scott (1991) found that female Brown-headed Cowbirds lay their eggs an average of 9 min before sunrise, whereas seven potential host species all lay their eggs after sunrise. Shiny Cowbirds (*M. bonariensis*) and, possibly, the nonparasitic Bay-winged Cowbird (*M. badius*) also sometimes lay before sunrise (see Scott 1991), but the data available to Scott (1991) were insufficient to conclude that sunrise laying is an adaptation for brood parasitism. There were no direct observations of laying for the Bronzed Cowbird (*M. aeneus*). Carter (1986) stated only that this brood parasite lays "during dawn hours". Here we report, to our knowledge, the first recorded observations of laying times for the Bronzed Cowbird.

METHODS

Our observations were made at the Welder Wildlife Refuge in San Patricio County, Texas (28° 0′ N, 97° 5′ W) in 1994. Both Bronzed and Brown-headed cowbirds were present during the breeding season. After locating a nest at which a host apparently had not completed laying, we watched it the following morning beginning approximately 30 min before sunrise. We hid far enough away so that hosts or visiting cowbirds were not disturbed. The nests were observed with binoculars when necessary. Sunrise (SR) times were obtained from the website of the United States Naval Observatory Astronomical Applications Department (http://aa.usno.navy.mil/AA/). All times are Central Standard Time.

RESULTS

Three Bronzed Cowbird laying events were observed directly, all at Northern Cardinal (*Cardinalis cardinalis*) nests. On 30 May 1994 we located a cardinal nest (94-16) containing one cardinal egg. The following morning, BDP arrived at this nest at 05:14 (SR − 20 min) and found a Bronzed Cowbird egg that was slimy, suggesting it had been laid recently, plus one cracked cardinal egg. Later the same day the nest contained two cardinal eggs plus the cowbird egg. At 05:06 (SR −

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28 min) on 1 June the nest contents were the same, but by 05:14 a second Bronzed Cowbird egg had been laid. Later that day, the damaged cardinal egg was gone and a third cardinal egg had been laid. On the morning of 2 June the female cardinal was accidentally flushed from the nest, and the nest contents were the same as the day before. At 05:14 (SR − 20 min) BDP watched a female Bronzed Cowbird fly directly to the nest, lay an egg, and fly away in 5–10 s. BDP left momentarily at 05:15, but upon returning at 05:19, found four Bronzed Cowbird eggs in the nest. No bird species is known to lay more than one egg per day (Sturkie 1976), thus we assumed a second female had laid an egg in this nest.

Nest 94-22 was found with one cardinal egg on 14 June 1994. On 15 June a female Bronzed Cowbird looked into the nest at 5:19 (SR − 14 min), but she did not lay. On 16 June K. Stewart observed two Bronzed Cowbirds parasitize this nest, one at 05:17 (SR − 16 min) and a second at 05:19 (SR − 14 min). Neither cardinal was present during the laying events and both laying bouts lasted 5–10 s. In addition to the three laying events observed, we estimated the two other laying times by taking the midpoints of repeated visits to the nests (Scott 1991) and found that Bronzed Cowbirds laid their eggs 18.2 min ± 1.7 SE before sunrise (range, SR − 14 to 24 min).

DISCUSSION

Like the Brown-headed Cowbird, and sometimes the Shiny Cowbird (Scott 1991), Bronzed Cowbirds lay prior to sunrise and, similar to other brood parasites, they lay rapidly (Sealy et al. 1995). It is undoubtedly advantageous for brood parasites to lay their eggs when hosts are absent and to lay as rapidly as possible (reviewed in Sealy et al. 1995). Indeed, Neudorf and Sealy (1994) found that hosts of the Brown-headed Cowbird at Delta Marsh, Manitoba, that did not roost on their nests overnight typically arrived at the nests in the morning after cowbird parasitism would have occurred. Female Bronzed Cowbirds have been observed entering host nests at various times of the day, but it is unknown whether eggs were laid (Thurber and Villeda 1980; T. Brush, pers. comm.). While it is possible that eggs were laid during these visits, these females may have been inspecting nests (see below), or they may have punctured host eggs (Carter 1986, Peer 1998).

The female Bronzed Cowbird observed visiting a nest prior to sunrise without laying may have been inspecting this nest to determine whether it was active and ready to be parasitized (see also Mayfield 1961, Nolan 1978). This nest was parasitized by two Bronzed Cowbirds the following morning. The cowbirds were clearly aware of the nest beforehand because they flew directly to it. Similar behavior has been reported for Brown-headed Cowbirds (Hann 1941, Neudorf and Sealy 1994).

The three cowbird species mentioned above are the only icterids known to lay before sunrise. The nonparasitic Bay-winged Cowbird may also lay prior to sunrise (see Scott 1991). Direct observations of laying by the Bay-winged, Giant (*Scaphidura oryzivora*), and Screaming (*M. rufoaxillaris*) cowbirds are required before it can be concluded that pre-sunrise laying in cowbirds is an adaptation for parasitism.

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Temporal Differences in Point Counts of Bottomland Forest Landbirds

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ABSTRACT.—We compared number of avian species and individuals in morning and evening point counts during the breeding season and during winter in a bottomland hardwood forest in west-central Mississippi, USA. In both seasons, more species and individuals were recorded during morning counts than during evening counts. We also compared morning and evening detections for 18 species during the breeding season and 9 species during winter. Blue Jay (*Cyanocitta cristata*), Mourning Dove (*Zenaida macroura*), and Red-bellied Woodpecker (*Melanerpes carolinus*) were detected significantly more often in morning counts than in evening counts during the breeding season. Tufted Titmouse (*Baeolophus bicolor*) was recorded more often in morning counts than evening counts during the breeding season and during winter. No species was detected more often in evening counts. Thus, evening point counts of birds during either the breeding season or winter will likely underestimate species richness, overall avian abundance, and the abundance of some individual species in bottomland hardwood forests. *Received 15 Nov. 1997, accepted 20 Aug. 1998.*

Improvement and standardization of assessment techniques for monitoring bird populations has received considerable attention (e.g., Ralph et al., 1993, 1995a, b; Hamel et al. 1996). Although most studies of avian population assessment techniques have focused on breeding birds, some have evaluated winter bird populations (Rollfinke and Yahner 1990; Gutzwiller 1991, 1993a, b). Detecting statistically significant changes in avian populations may require an extensive monitoring network (Smith et al. 1993, Hamel et al. 1996). To achieve monitoring objectives using limited resources, protocols that reduce costs and maximize efficiency are required (Smith et al. 1993). Unfortunately, many factors that influence survey efficiency are beyond the control of investigators. For example, detection varies among species, among census techniques (e.g., Grue et al. 1981, Rollfinke and Yahner 1990), and may be influenced by physical or biological factors (Gutzwiller 1993a, b).

If detection probabilities were constant over time, the efficiency of avian surveys could be increased by providing a greater window of opportunity during which surveys could be conducted. However, most species exhibit diel and seasonal variation in detectability. Thus, to optimize sampling effort and reduce sampling variances, monitoring should be focused on periods when species are most frequently detected (Gutzwiller 1993a).

To assess optimal periods of detection, investigators have compared point counts from different times of the morning during the breeding season (Shields 1977, Grue et al. 1981, Robbins 1981, Skirvin 1981) or winter (Gutzwiller 1993a). Only Rollfinke and Yahner (1990), using transect counts, compared morning counts to evening counts during winter. Although birds are generally assumed to

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be more detectable during morning than during evening, we suspected that some species were equally detectable during both periods. If true, monitoring efforts that focused only on these species could greatly expand the time during which surveys could be conducted. To evaluate the differences in detection of avian species between morning and evening, we conducted paired morning and evening point counts during the breeding season and during winter. In this paper, we report the resulting estimates of avian species richness, overall abundance, and abundance of selected species. We also assess the relationship between detection of individual species and the observed variation between morning and evening counts.

STUDY SITE AND METHODS

Point counts were conducted on the 1050 ha Delta Experimental Forest, near Stoneville, Mississippi (33° 29′ N, 90° 55′ W). Surrounded largely by agriculture, this bottomland hardwood forest was heavily logged from 1910 to 1920 with additional research and commercial harvests continuing though the 1960s. There was no timber harvest on Delta Experimental Forests between the early 1960s and the time of this study.

We conducted morning and evening point counts during the breeding season (30 May–12 June 1991; 8–21 May 1992) and winter (4–14 February 1991; 9–29 January 1992) at 25 stations in each of 4 forest stands. Forest stands were similar in habitat but were subjected to different silvicultural management. We generally followed standardized protocols for conducting point counts (Ralph et al. 1993, Hamel et al. 1996) but used 4-min sampling periods instead of 5-min and 20-m fixed radius circular plots instead of 50-m. We reduced the sampling period based on species detection curves from preliminary survey data and we restricted the plot radius to 20-m because of a concurrent effort to model habitat using these same data. Points were visited so that each visit occurred at a different time during the 3-h periods following sunrise (morning) and preceding sunset (evening). Over the two years of this study, we made a total of 10 morning and 10 evening visits to each of the 4 stands during the breeding season. Within the same time interval, we made a total of 6 morning and 6 evening visits to each stand during winter. Detection probability (Gutzwiller 1993a) was estimated for each species as the proportion of total point counts during which the species was detected. During the breeding season and during winter we compared the number of species and individuals detected during morning and evening visits using a split plot, repeated measures analysis of variance; each stand (an experimental design block) was split into morning and evening treatment periods with visits (dates) constituting the repeated measure. All statistical analysis were performed using the SAS System for Windows (Release 6.11, SAS Institute, Inc., Cary, NC, USA). We subsequently compared the abundance of selected individual species between morning and evening counts using the same experimental design. However, individual species abundances were compared only if the overall variability of the species allowed detection of at least 0.25 individuals when the power of the test ($1 - \beta$) was at least 0.80 with $\alpha = 0.10$ (Hamel et al. 1996). Furthermore, because we conducted multiple tests when comparing individual species, we used Bonferroni's correction which reduced the probability required for significance of these tests to $\alpha \leq 0.006$.

RESULTS

We recorded 57 forest landbird species during the breeding season and 36 species during the winter. More species ($F_{1,3} = 383.35$, $P < 0.01$) and total individuals ($F_{1,3} = 597.38$, $P < 0.01$) were detected in morning counts ($\bar{x} \pm$ SE; 10.05 ± 0.06 species, 11.66 ± 0.08 individuals) than in evening counts ($\bar{x} \pm$ SE; 7.77 ± 0.07 species, 8.46 ± 0.09 individuals) during the breeding season. During winter, we again detected more species ($F_{1,3} = 82.38$, $P < 0.01$) and total individuals ($F_{1,3} = 26.59$, $P = 0.01$) in morning counts ($\bar{x} \pm$ SE; 6.12 ± 0.07 species; 9.36 ± 0.14 individuals) than in evening counts ($\bar{x} \pm$ SE; 4.44 ± 0.08 species, 6.45 ± 0.13 individuals).

During the breeding season, 16 of 57 species met our criteria for comparing morning and evening counts of individual species (Table 1). We detected significantly ($F_{1,3} \geq 46.83$, $P < 0.006$) more individuals during morning counts than during evening counts for four species: Blue Jay (*Cyanocitta cristata*), Tufted Titmouse (*Baeolophus bicolor*), Mourning Dove (*Zenaida macroura*), and Red-bellied Woodpecker (*Melanerpes carolinus*). No significant differences ($P > 0.01$) were detected between morning and evening counts for the other 12 species (Table 1). Of the 11 species eligible for comparison during winter, only Tufted Titmouse was detected significantly ($F_{1,3} = 50.6$, $P < 0.006$) more during morning than during evening. As with the breeding season, the detection of the remaining species did not differ significantly ($P > 0.01$) between morning and evening counts (Table 1).

Detection probability of individual species ranged from less than 0.01 to 0.70 during winter and from less than 0.01 to 0.82 during the breeding season. There was a significant cor-

TABLE 1. Abundance ($\bar{x} \pm$ SE) and detection probability of individual species from morning and evening point counts conducted during the breeding season and during winter of 1991 and 1992 on Delta Experimental Forest, Stoneville, Mississippi, USA.

Species	Breeding season			Winter		
	Morning abundance $\bar{x} \pm$ SE	Evening abundance $\bar{x} \pm$ SE	Detection probability	Morning abundance $\bar{x} \pm$ SE	Evening abundance $\bar{x} \pm$ SE	Detection probability
Mourning Dove (*Zenaida macroura*)	0.688 ± 0.021[a]	0.412 ± 0.018	0.475[c]	—[b]	—[b]	0.044
Yellow-billed Cuckoo (*Coccyzus americanus*)	0.525 ± 0.020	0.430 ± 0.018	0.419	0	0	0
Red-headed Woodpecker (*Melanerpes erythrocephalus*)	—[b]	—[b]	0.078	0.309 ± 0.024	0.422 ± 0.030	0.227[c]
Red-bellied Woodpecker (*Melanerpes carolinus*)	1.279 ± 0.023[a]	0.865 ± 0.025	0.762[c]	1.208 ± 0.034	0.870 ± 0.030	0.695
Downy Woodpecker (*Picoides pubescens*)	0.468 ± 0.018	0.422 ± 0.019	0.404	0.497 ± 0.020	0.437 ± 0.023	0.400
Northern Flicker (*Colaptes auratus*)	—[b]	—[b]	0.024	0.612 ± 0.022	0.703 ± 0.026	0.396[c]
Great-crested Flycatcher (*Myiarchus crinitus*)	0.247 ± 0.015	0.194 ± 0.013	0.208	0	0	0
Blue Jay (*Cyanocitta cristata*)	0.645 ± 0.022[a]	0.458 ± 0.021	0.456[c]	0.853 ± 0.032	0.235 ± 0.022	0.388
Carolina Chickadee (*Poecile carolinensis*)	0.877 ± 0.029	0.574 ± 0.026	0.528	1.048 ± 0.039	0.750 ± 0.033	0.574
Tufted Titmouse (*Baeolophus bicolor*)	1.203 ± 0.028[a]	0.814 ± 0.029	0.666[c]	0.866 ± 0.034[a]	0.320 ± 0.023	0.423
Carolina Wren (*Thryothorus ludovicianus*)	1.200 ± 0.027	0.822 ± 0.026	0.704[c]	0.655 ± 0.028	0.300 ± 0.021	0.376
Wood Thrush (*Hylocichla mustelina*)	0.383 ± 0.019	0.387 ± 0.019	0.322	0	0	0
American Robin (*Turdus migratorius*)	—[b]	—[b]	0.003	1.276 ± 0.088	0.900 ± 0.050	0.543[c]
White-eyed Vireo (*Vireo griseus*)	0.212 ± 0.014	0.152 ± 0.012	0.168	0	0	0
Red-eyed Vireo (*Vireo olivaceus*)	0.276 ± 0.015	0.134 ± 0.011	0.196	0	0	0
Yellow-rumped Warbler (*Dendroica coronata*)	0	0	0	0.992 ± 0.048	0.717 ± 0.015	0.436
Prothonotary Warbler (*Protonotaria citrea*)	0.246 ± 0.016	0.097 ± 0.010	0.155	0	0	0
Summer Tanager (*Piranga rubra*)	0.331 ± 0.016	0.490 ± 0.020	0.360	0	0	0
Northern Cardinal (*Cardinalis cardinalis*)	1.315 ± 0.025	1.112 ± 0.026	0.819[c]	—[b]	—[b]	0.094
Indigo Bunting (*Passerina cyanea*)	0.536 ± 0.021	0.459 ± 0.020	0.418	0	0	0
White-throated Sparrow (*Zonotrichia albicollis*)	0	0	0	0.127 ± 0.029	0.171 ± 0.036	0.050

[a] Mean number of detection greater ($P < 0.006$) for morning counts than for evening counts.
[b] Morning and evening counts not compared.
[c] Detection probability differs significantly between breeding season and winter (test of difference between two proportions, $z > 1.96$, $P < 0.05$).

relation between detection probability and variation in abundance during the breeding season ($r_s = 0.74$, $P < 0.01$) but not during winter ($r_s = 0.32$, $P > 0.05$). Six of 11 species found at our study site throughout the year, Red-bellied Woodpecker, Downy Woodpecker (*Picoides pubescens*), Blue Jay, Tufted Titmouse, Carolina Wren (*Thryothorus ludovicianus*), and Northern Cardinal (*Cardinalis cardinalis*), had greater detection probabilities ($P < 0.05$) during summer (Table 1). Conversely, Red-headed Woodpecker (*Melanerpes erythrocephalus*), Northern Flicker (*Colaptes auratus*) and American Robin (*Turdus migratorius*) had greater detection probabilities during winter.

DISCUSSION

During the breeding season, morning point counts yielded more species and more individuals than did evening counts. Furthermore, when significant differences existed for individual species, morning counts were consistently higher than evening counts. Forest landbirds have long been presumed to be more detectable during early morning than at other times of the day and many observers restrict breeding bird censuses to morning hours (Skirvin 1981). In studies of diel variation (Shields 1977, Skirvin 1981), more species and individuals were detected during the initial 2 h after sunrise than at other times. In floodplain forests, Robbins (1981) found that, although the total number of birds recorded diminished beyond 2 h after sunrise, the number of species detected remained nearly uniform for up to 5 h after sunrise. Although there have been few comparisons of early morning and late evening censuses, Grue and coworkers (1981), working in desert habitats during the breeding season, found more species and individuals during morning point counts than during evening counts. Our data provide further empirical evidence to support presumed temporal differences in avian detections between morning and evening counts during the breeding season.

During winter, we also detected more species and individuals on morning point counts than on evening counts. Rollfinke and Yahner (1990) also reported more species and more individuals on early morning transects than on evening transects during winter. Although we detected only Tufted Titmouse significantly more on morning counts than on evening counts during winter, Gutzwiller (1993a) found that five species had higher detection probabilities on point counts between 07:00 and 13:45 than at other times of the day. Overall, our data suggest that evening point counts during either the breeding season or winter will probably underestimate species richness, overall avian abundance, and the abundance of at least some species in bottomland hardwood forests.

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Ornithological Literature

Edited by William E. Davis, Jr.

THE BIRD COLLECTORS. By Barbara and Richard Mearns. Academic Press, San Diego and London. 1998: xviii + 472 pages, many unnumbered figures, 4 maps of expedition itineraries. $49.95 (cloth).—This is the third book by the Mearnses in 10 years. The first two consisted of biographies of persons after whom birds have been named; first, for the Western Palearctic ("Biographies for bird watchers", 1988, reviewed in *Wilson Bulletin* 101:658–659), and then for North America ("Audubon to Xantus", 1992, reviewed in *Wilson Bulletin* 105:701–702). Richard is a countryside ranger in Scotland; Barbara is a professional occupational therapist, but in recent years has spent more and more time on her avocation, biohistorical research.

Their new book, although biographical in large part (and thus overlapping slightly with the first two books), has quite a different balance. The Mearnses are well aware that the collecting of bird specimens in the late 20th Century is subject to much debate, often acrimonious. The arguments and the social and political pressures of the current anti-collecting camp are phenomena seldom if ever faced by the historical collectors whose exploits form most of the book's subject matter. The Mearnses make their position plain in a brief preface; neither of them has ever deliberately killed a bird (they salvage accidentally killed birds for the Royal Museum of Scotland). They point out, however, that anyone who, in their words, turns "pale at the mere thought of killing birds" must realize that "anyone who drives a car, uses products of the petrochemical industries, owns a cat, has glass in the windows of their home, buys paper, or consumes electricity will be responsible for killing birds." This subject is dealt with at greater length in their Chapter 17, "The importance of old and new bird collections," which relies heavily on the important paper by Remsen (1995).

The first three chapters bounce around a good bit, dealing with reasons for killing birds other than for museum collections, bird books and journals, human casualties, labeling and note-taking, problems in the field, in shipment of specimens, and in the museum, etc. By the fourth chapter, the emphasis becomes primarily historical, reviewing collecting and collectors chronologically. But the arrangement is not strictly chronological as a whole; chapters on specific kinds of collectors are internally chronological. Examples include "Bird artists as collectors," "Government-sponsored collecting," "Army officers," "The medical profession," and "Clergymen and missionaries." A chapter entitled "The great accumulators" treats the owners of large private collections, beginning with the 13th Earl of Derby (1775–1851) and ending with the notorious Colonel Richard Meinertzhagen (see Knox 1993). A chapter on "The professional field collectors" is a hodgepodge, including scientists such as Alfred Russell Wallace, whose collections were indeed sold, and contract collectors working for museums, such as Rollo Beck. This chapter is much too short, as major portions of the holdings of several of the large museums were made by collectors under contract; in South America, for example, some of the most prolific were Samuel Klages, the Steinbachs (father and son), M. A. Carriker, Jr., and more recently William H. Partridge. Of these, only Carriker is mentioned, thrice; half of a sentence in the "Professional field collectors" chapter and half of a paragraph on his two wives in a chapter on "Women in the field"!

The Mearnses admit in their Preface that their "approach has been rather Anglo-centric," after which they list by name 17 "great collectors [who] have been omitted or not mentioned in detail"—the third reference to Carriker is the presence of his name in this list. The relative neglect of some parts of the world is obvious all through the book, and I'm not sure this can be wholly excused by their admission quoted above. They appear to have been obsessed by the history of collecting in central Asia, as this is the subject of a 27-page chapter called "Terra Incognita", in which 7½

pages, a map and three portraits are devoted to the exploits of General Nicholas M. Prjevalsky (of Prjevalsky's Horse), and slightly more text plus a map and a portrait to those of Armand David (of Père David's Deer). Surely most of the South American continent was at least as "incognita".

In the "Professional field collectors" chapter, Lord Rothschild is quoted as having stated that William Doherty (1857–1901) was "unquestionably the best collector for the last fifty years." To anybody who has seen bird skins from Doherty's expeditions, this statement is incomprehensible; he never learned to skin birds for himself, turning them over to Indian servants, according to the Mearnses. Carnegie Museum of Natural History has a collection Doherty made in Kenya six months before his death in 1901 (Holland 1905). The skins are mediocre and the original labels bear nothing but a pencilled sex mark; the data ("10 miles W of Mombasa, September–October 1900") were apparently supplied by Doherty to Dr. Holland, Director of the museum, who had purchased the collection. All of this suggests that the Mearnses were probably correct in suggesting that Rothschild's high praise of Doherty may have been based on his "services to entomology."

A chapter on "Women in the field" contains 9 short biographies. Of the women thus honored, only 3 [Emilie Snethlage, Elizabeth Kozlova, and Beryl P. (Pat) Hall] contributed to ornithology primarily through their collecting activities, at a level comparable to that of most of the males featured in the rest of the book. Here is where we find the Mearnses' most appalling omission; the late Maria Koepcke (1924–1971), whose name appears as the only woman in the Preface list of collectors who "deserve more space than we could give them". Maria Koepcke may justifiably be said to be one of the true pioneers in the 20th Century study of the ornithology of Peru, a small country whose avifauna numbers about 1⅓ times that of the entire Palearctic. She and her husband Hans-Wilhelm, trained as a hydrobiologist, founded Casa Humboldt (=Humboldt House) in Lima in 1957; this became the convenient base for many expeditions throughout Peru involving scientists from several nations. Maria conducted avifaunal surveys in areas ranging from the desert coast to the Amazonian rain forest. Her bibliography lists 29 titles, plus 12 co-authored with her husband. She described 3 new species and 13 new subspecies.

An Appendix lists, in sequence of size, the world's 69 largest collections of bird specimens, together with the most significant components included therein. Unfortunately there are many errors and omissions in this list, partly because for some museums the authors' information was a quarter-century out of date, based on Banks and coworkers (1973). It is a pity that they felt no need to enter into correspondence to get more recent figures. Attribution of components is irregular; parts of the dismantled collections of the Cleveland Museum of Natural History, for example, are listed for the Field Museum; the Museum of Zoology, University of Michigan; and the Peabody Museum, Yale University, but *not* the Carnegie Museum of Natural History, which may have the largest number of former Cleveland birds. No components are listed for the Delaware Museum of Natural History, which holds one of the most important U.S. collections of Philippine birds, and much of the former collections of John E. duPont, George M. Sutton, and Allan R. Phillips. Numerous other omissions could be mentioned, such that this Appendix is not as valuable as it could have been.

Any heterogeneous work of this sort is bound to induce comments and corrections. A few are listed below:

p. 13. The authors mention the extinction of the endemic flowerpecker (*Dicaeum quadricolor*) of Cebu owing to the deforestation of that Philippine island; in fact, no fewer than 9 endemic forms of Cebu were thought to have been extirpated (Rabor 1959), although small remnant populations of a few of these have subsequently been found.

p. 111. The authors refer to "remote, little-known islands such as Whitsunday Atoll, Clarion Island and the Revillagigedo group." Clarion is, in fact, one of the islands in the Revillagigedo group.

p. 149. For a more complete account of the fate of the Gould Australian collection, see Meyer de Schauensee 1957.

p. 182. The Ruwenzori mountains are on the western, not the eastern border of Uganda.

p. 244. British writers should know that the

authorship of the classical *Handbook of British Birds* was in the sequence Witherby, Ticehurst, Jourdain and Tucker; the Mearnses list Jourdain last.

p. 270. A comment would have been appropriate after the statement about Prjevalsky's first expedition; "there would have been more [bird specimens] but most were moulting so nine-tenths of all of the birds shot were discarded." This atrocious practice has, of course, proved to be the bane of students of molts and plumages; I encountered the same kind of statement in connection with some 19th Century British collectors of Philippine birds.

p. 366. Brina Kessel and I have been friends and colleagues for fifty years, but I can't understand the rationale for including her in a book about collectors. The Mearnses mention that "her first specimen-based research was for her Ph.D. dissertation on European Starlings and involved the preparation of over 500 skins." True enough, except that the majority of the starlings were collected and prepared by Robert W. Dickerman.

I need hardly say that any reader of this book will find, as I did, that the descriptions of the exploits of many collectors previously known to us as little more than names attached to bird species have been brought to vivid life by the Mearnses. Their book is highly readable, and their attitude toward collecting as fair-minded as one might ask of writers not directly involved themselves in collecting.

I am indebted to Manuel Plenge for sending me biographical materials on Maria Koepcke.—KENNETH C. PARKES.

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LIFE OF THE FLYCATCHER. By Alexander F. Skutch. Illustrated by Dana Gardner. University of Oklahoma Press, Norman, Oklahoma. 1997: xiii + 162 pp., 16 color plates, 32 black-and-white drawings, 4 tables, bibliography, index. $40.00. ISBN 0-8061-2919-0.—Alexander Skutch brings forth a popular review of the Tyrannidae in *Life of the Flycatcher.* This volume continues Skutch's *Life of . . .* series, each reviewing variation in life history within a bird family (e.g., Tanager, Pigeon, Woodpecker, Hummingbird). The Tyrannidae, subject of this current volume, is a large family (380 species) of suboscines limited to the New World. The text is successful in showing the great degree of diversity displayed by this family. If your knowledge of New World flycatchers is limited to North American species, the diversity described for the family in *Life of the Flycatcher* will amaze you. The text may offer inspiration for evolutionary inquires and directions for further study.

The text begins with an overview of the family, and continues with chapters on food, daily life, song, courtship, nest, eggs, young and breeding success. Skutch's personal experience with this group during his long career in the American tropics is evident. The book ends with 138 references organized by chapters and an index. The bibliography provides some direction to seeking further information.

Skutch takes some exception to the illogic often apparent in birds' names and uses "flycatcher" in common names rather than various forms of "tyrant" (as in "marsh-tyrant" or "tyrannulet"); this practice may delay tracking down specific species in other texts. The only error of some note I found was in the index: Alder Flycatcher was identified as "*Empidonax minimum.*"—PETER E. LOWTHER.

A NEOTROPICAL COMPANION: AN INTRODUCTION TO THE ANIMALS, PLANTS, AND ECOSYSTEMS OF THE NEW WORLD TROPICS. Second edition, revised and expanded. By John Kricher. Princeton University Press, Princeton, New Jersey. 1997: 451 pp., 177 color photographs, 86 line drawings. $29.95 (cloth).—This sturdy vol-

ume accompanied me for 10,000 miles this spring, enlightening me during airport vigils, on long flights, and during hot nights in Guatemala and elsewhere. Except for a warped cover it is still in excellent condition. Despite many prior trips to the American tropics, I found this book fascinating reading as well as a valuable reference to other literature sources.

This is a series of authoritative essays on tropical ecology, organized in 14 chapters and followed by an Appendix, a list of Acronyms, a Glossary, 35 pages of References, and an Index that includes every species, genus, and topic mentioned. The Appendix, "And, Hey, Let's be Careful Out There," should catch the reader's eye before (s)he leaves home. If you are a tropical bookworm you will appreciate the miniabstracts of his 40 book-length references.

Chapters are arranged in a logical sequence, beginning with textbook descriptions of climates and ecosystems, and rainforest structure, diversity, and function. Chapters on evolutionary patterns and coevolution/ecology of fruit track relationships among animals and plants from the research of Darwin to investigators of the mid 1990s. After brief chapters on the Neotropics as a pharmacy and on living off the land, are chapters on ecosystems (rivers, mountains, savannas, dry forests, mangroves, coral reefs) and on Neotropical birds and mammals, culminating with a lively discussion on deforestation and biodiversity. A strong conservation theme teases the reader to take appropriate action.

Professor Kricher writes in an easy conversational style, tempting the student, the researcher, or the vacationer to read on and on. His wide field experience in Central and South America, his extensive knowledge of the tropical literature, his long academic career, and his gift for writing combine to make this publication a gem for the tropical explorer. Statements in the text are supported by close to a thousand references to the scientific literature. Terms defined in the glossary are italicized in the text. Dozens of delightful line drawings of birds, mammals, and lesser life forms from the pen of Ted Davis grace the pages. A new feature in this edition is a collection of 177 color photos, all cross-referenced from the text.

I was shocked to read in the conversion table (p. xviii) that 1 square mile = 2,590 square km and (p. 35) that 1 cm = 2.5 in. And I regret to report 9 scientific names of birds were misspelled one or more times, including "Beautiogallus" (3 times). These preventable accidents aside, the book is a goldmine of information that will greatly enrich one's tropical experience.

The Neotropical Companion should be in every high school and college library, in the travel section of your public library, and in the carryon luggage of all students and birders bound for the American tropics.—CHANDLER S. ROBBINS.

THE BIRDS OF ST. LUCIA, WEST INDIES. By Allan R. Keith. British Ornithologists' Union, c/o The Natural History Museum, Tring, Herts HP23 6AP, United Kingdom. 1997: 176 pp., 40 color plates with captions, 7 text figures, 3 tables, 7 appendices, 14 £ (cloth).—In recent years, the British Ornithologists' Union has done the ornithological community a tremendous service by sponsoring the production of a variety of check-list style books specializing on unusual or exotic regions of the world. Compared to Gambia, Nigeria, Cyprus, The Philippines, or even the Southern Bahamas, St. Lucia is a tiny area that supports a fairly small avifauna. Nevertheless, this is a splendid book that provides both the detailed observational information one expects from a check-list plus a vast amount of other information that shows us why St. Lucia is an important place in the ornithological world.

The nitty-gritty of any check-list lies in its species accounts, which in this case cover 162 species that currently occur on St. Lucia or have reliable records from the past. The author does these accounts in a spartan 60 pages. To this can be added short appendices covering species of uncertain occurrence, where museum specimens from St. Lucia reside, recoveries of banded birds in St. Lucia, a gazetteer, and the origins of resident breeding birds. A major appendix (18 pages) provides more information on the 3 endemic species and 3 endemic sub-species found on the island. The author seems to have left no leaf, library, or

museum unturned in gathering all the details available about St. Lucian birds.

Were the above material all of the book, I would readily recommend it for anyone planning a visit to the island, but I would question its value to the general reader. Allan Keith's introductory material (9 chapters adding up to 60 pages) does an excellent job of introducing the island on which the bird records were made. Chapters include political history, geology and geography, climate, vegetation, history of ornithological exploration, migration, breeding, zoogeography and conservation. All of this information makes the avifauna of St. Lucia come much more alive as part of one island within the West Indian region. Keith also does an outstanding job of pointing out the unusual role this island has played in West Indian conservation, as a result of the combined efforts of a local biologist (the late Gabriel Charles) and an English vagrant (Paul Butler) in developing a conservation plan that was very successful on St. Lucia and has been exported elsewhere.

This combination of detailed observational work in the species accounts with the broad biogeographic and ecological perspective found in the introduction allows the reader to not only find out what species occur on St. Lucia, but to get a feeling about why it is this number and how the island compares to its neighbors. The author's synthesis of current scientific thought is exemplary (although a few sections may need to be revised when the current work being done on molecular genetics of West Indian birds is finally released). This is a great way to both find out what is on St. Lucia and to get a bit of a feeling about why this is so.—JOHN FAABORG.

MUNIAS AND MANNIKINS. By Robin Restall, illus. by the author. Yale University Press, New Haven, Connecticut. 1997: 264 pp., 16 colored plates with captions, 64 color plates with measured drawings, innumerable text figures. $60.00—Robin Restall is a lifelong enthusiast of caged finches, whose employment with an international advertising agency has taken him to most parts of the world where he could learn about many of the species of finches in their native contexts. His particular interest is with the genus *Lonchura,* which now includes all of the birds traditionally referred to as munias, mannikins, and the Java and Timor Sparrows which were formerly considered in the genus *Padda.*

This is a masterful collection of virtually every thing known about this assemblage of estrildine finches. The book starts off with a review of the taxonomy and relationships of the genus *Lonchura,* continues with an overview of their natural history, and concludes with a detailed accounting of all pertinent information about each individual species (including one apparently new, undescribed species).

Each species account includes headings for field characters, status, habitat, habits and behaviors, food and feeding, movements, call, song, courtship and display, breeding, distribution, description (including all known subspecific variants), hybrids, conservation, and a list of relevant references. There are color plates for each species, showing all of the most obvious sex, age, and geographic variants and an even more impressive collection of color plates of measured drawings that show the dorsal and ventral views with one wing extended.

I found this to be an excellent summary of information on a group of birds about which I knew relatively little. Yale University Press has done a fine job of editing (I found very few typographic errors), and the color reproduction of the plates appears to be first-rate. I recommend the volume highly.—HERBERT T. HENDRICKSON.

FOREST PATCHES IN TROPICAL LANDSCAPES. By John Schelhas and Russell Greenberg, Eds. Island Press, Washington, D.C. 1996: 426 pp., maps, tables, black-and-white figures. $30.00 (paper).—It is obvious to anyone who studies any aspect of global tropical ecology that forest fragmentation is increasing annually. The complex ecological effects of fragmentation are only now becoming known, an increasing database generated from the efforts of numerous researchers in tropical regions around the world. Most tropical ecologists are familiar with the ongoing study known now as the Biological Dynamics

of Forest Fragments Project, located north of Manaus, Brazil, but this multi-authored volume includes data from numerous studies in other regions (as well as one chapter dealing with the BDFFP).

The book is divided into four parts: changing forests, regional landscapes, human dimensions, and management. The introduction, authored by the editors, provides a concise but thorough overview of the issues covered in depth throughout the volume. Birds are the focus of but one of the 19 chapters, but are discussed to varying degrees in numerous other chapters. Most of the chapters deal with South and Central America though there is one chapter on Africa, one largely on Indonesia, and one on India. Each chapter is referenced from the primary literature.

This volume, broad in scope, and excellently edited, is an important resource for tropical ecologists, particularly those whose research is focused on biodiversity preservation and ecologically sound management policies.—JOHN C. KRICHER.

WHERE TO WATCH BIRDS IN ASIA. By Nigel Wheatley. Princeton Univ. Press, Princeton, New Jersey, 1996: 463 pp., 51 line drawings, 8 figs., 105 maps. $35.00.—This remarkable book compresses an impressive amount of birding data from our largest continent into a relatively compact volume. Asia (including the island nations of Indonesia and the Philippines) harbors just under 2,700 bird species. Considering that various parts of the continent have been off limits—or inaccessible—to outsiders for much of our lifetimes, I was delighted to see how many places have now been surveyed by keen birders. The author is to be congratulated on gathering these scattered data into one volume. The book is not meant as an encyclopedic reference to all sites or to all species in a given country and the author rightly suggests that the information may be best used as a first "guiding light", a starting point in travel planning. The book fills this function admirably and by studying material presented here you can quickly focus on desirable Asian locations and the species found there. The format is appealing and easy to follow, while the text, composed in a clear 9 point Cheltenham Light, is remarkably free of typographical errors.

The book is divided into three parts: a general introduction, the main text (organized by countries), and additional suggestions and indexes. The introduction is necessarily brief but explains the book's layout and then provides much useful information relating to birds and birding in Asia and includes notes on habitat diversity, bird diversity (at the family and species levels), and how Asia compares with other continents (400 species more than Africa and 400 less than South America). Conservation is given a separate six paragraph section where Wheatley is brave enough to identify human population growth as a major conservation problem and to call for growth stabilization, or better yet, "we should aim to reduce" population growth. Under General Tips we learn of familiar techniques for good birding (some Asian birds are very shy) and of various dangers to travelers. Altitude sickness (in the higher Himalayas and Tibet) is mentioned but I find the subject treated too lightly. The recommended one night at 3000 m. (9,843′) before ascending to 4500 m. (14,764′) the next night is far too fast for many people hiking in the Himalayas. Similarly, it is suggested that if one "turns blue and coughs up pink mucus" one should immediately descend to below 3000 m. (9,843′). Actually one should have descended well before this grim stage is reached. Keep in mind, that "descending immediately" from some locations in Tibet is not possible.

In the main text, forty countries are summarized in varying detail (one paragraph for the Maldives to 57 pages for Indonesia; North Asia is not covered). English names follow those used by James Clements *Birds of the World: A Check List* (Fourth edition, 1991 and Supplements) and is a most useful correlation. Yet it is a pity that, except for 189 species given in an appendix, scientific names are not recorded somewhere in the book.

Each country report follows a standard format that starts with a general map, followed by a summary and then short notes on size, transport within the country, accommodations, health and safety, climate and timing, habitats, conservation, special birds, a note on endemics, and how many species one might expect

to see in a stated time. These sections are helpful planning tools. Accommodations and travel within the country are only lightly touched upon as vast descriptions are available in various general guides: accommodations mentioned are usually aimed at the individual traveling on a limited budget.

Following this general introduction, important birding sites are covered in a clear format. This material starts with an overall note and sometimes a map (of some 250 sites, 184 are not mapped) and then moves to a list of endemics seen at that particular site, followed by specialties, others, and finally other wildlife. Maps are so helpful that I would like to have seen more. The 51 line drawings (mostly of excellent quality) sprinkled throughout add visual appeal but do not enhance the usefulness of the text. Dropping line drawings to add maps would make the book more utilitarian albeit less attractive. Each country section ends with Additional Information that includes addresses of local bird clubs and nature societies, suggested readings, a complete list of all the country's endemics, and finally a paragraph giving near-endemics.

The book nears the end with yet additional addresses that include various general societies and clubs dealing with Asia, where one may obtain trip reports, and of 16 companies that do birding tours. After a selection of general book titles there are three pages of three-column fine print that give scientific names that correspond with Clements English names, and then with other English names used in Asian bird books (where these differ from the names used by Clements). The book concludes with two indexes.

With any volume of this magnitude readers will have varying opinions on the coverage and the presentation of the material. Perhaps the most serious omission of the book, to my mind, is that there is no clue as to the abundance of the species listed. Thus there is no distinction between a bird that has been seen once at that site or another that is recorded in numbers every day. Even a two-tier indication giving an "r" for very rare species and an "a" for an abundant species would be helpful. Similarly, some birds move seasonally and at times the text gives no idea as to when the bird might be at the site described. Tickell's Leaf Warbler (*Phylloscopus affinis*), for example, is listed for Corbett National Park (India), but for much of the year this migratory species is not in the park.

A curious paragraph called "near-endemics" appears at the end of each country summary. To save space, this section could easily be dropped or at least the definition of "near-endemic" tightened. It is hard to see how the Nepal Fulvetta (*Alcippe nipalensis*) is a "near-endemic" when it is listed for Bangladesh, Bhutan, Burma, Nepal, and northeast India.

As common to many first editions dealing with this much detail, there are a number of minor factual errors. For example, the Purple-rumped Sunbird (India) is listed under "more or less throughout" while the bird does not occur in the north. The plural of genus, p.25, is genera (not genuses). Similarly, Padang en route to Kirinci-Seblat National Park (Indonesia) is twenty-four hours (not six) by bus from Berestagi (Brastagi)—twenty-four, that is, if one is lucky. The Khunjerab Pass (Pakistan) is close to 16,000 feet (not 5575 m., 18,290′). On page 38 we learn that "most of the pristine forest which is left in the eastern Himalayas is in . . . Bhutan." In reality, there is far more eastern Himalayan forest in Arunachal Pradesh than in Bhutan but much of Arunachal is still off limits to outsiders. Namdapha National Park (India) is accorded "the greatest altitudinal range of any park in the world" but the Sagarmatha National Park and the Makalu-Barun National Park and Conservation Area in Nepal and the Quomolungma Nature Reserve in Tibet cover substantially more altitude than does Namdapha.

I fear this book will not sell well in the Maldives for on page 124 the Maldives disappears as a country only to resurface as a single paragraph under India. This treatment would surprise the citizens of this Indian Ocean nation. Agreed, the Maldives may not be particularly good for birding, but it has world class coral reefs and scuba diving and should be accorded full country status in the next edition.

These errors, however, are of a minor nature and do not detract from the importance of this effort and I strongly recommend the book to anyone who is even remotely thinking about those nearly 2700 Asian species that are just waiting to be seen.–ROBERT L. FLEMING, JR.

THE BIRDS OF SULAWESI. By Derek Holmes and Karen Phillipps. Oxford University Press, Oxford, U.K. 1997: 86 pp., 20 color plates illustrating 142 species, 22 black-and-white illustrations, one table. $24.95 (cloth).—The island of Sulawesi, part of the vast country of Indonesia, has only relatively recently been frequented by ecotourists and birders. Sulawesi is perhaps best known for Torajaland, where the local people practice elaborate funeral rites and the dead are placed in cliffside alcoves, commemorated with unique statues. Sulawesi was of great interest to Alfred Russel Wallace, as it sits almost astride "Wallace's Line," separating two biogeographic realms. The authors of this guide provide a brief table that compares the avifauna of Kalimantan, on one side of Wallace's Line, with Sulawesi, on the other side. They note that of the 380 species found on Sulawesi and its near neighbor islands (what the authors call the "Sulawesi region"), 96 are endemic to the region, and 115 are endemic to Indonesia.

While this guide is admittedly not comprehensive, it will prove very useful. The species treated are those most commonly seen, the illustrations are of good quality, and the text descriptions are adequate for identification. It would be helpful if some maps were included but none are. The authors state that "For the bird-watcher, Sulawesi is unequalled." That is certainly not true. Much of the island is devoted to rice farming and birds other than munias and some herons, are sparse. To get any real sense of the endemic avifauna one must visit one or more of the nature reserves and national parks, where some natural forest survives. Like much of the rest of Indonesia, roadside birding is disappointing, with a surprising paucity of birdlife.

The book is indexed and provides a checklist of resident land birds in the Sulawesi Faunal Region.—JOHN C. KRICHER.

THE WHOOPING CRANE: NORTH AMERICA'S SYMBOL OF CONSERVATION. By Jerome J. Pratt. Castle Rock Publishing, Prescott, Arizona. 1996: 171 pp., 46 photographs. $12.95 (paper).—The Whooping Crane (*Grus americana*) is a species that has been close to extinction throughout my lifetime and has rightly come to symbolize the conservation movement in North America. This book is an effort to relate the history of the species and the efforts made to prevent it from disappearing completely. The author, Jerome Pratt, was one of the charter members of the Whooping Crane advisory group established in 1956, and thus provides an "insider's" perspective on how the recovery project has unfolded. This may be the book's greatest short-coming. Saving endangered species appears to have some strong similarities to the making of sausage; you don't necessarily want to know everything that goes into it.

Pratt clearly has some strong opinions on how the recovery program should have proceeded, which differ from the way it actually unfolded. However, I found it difficult in reading the text to determine precisely what the points of difference were. Perhaps someone with less personal involvement would have been able to present a more clear explanation of exactly how the differing philosophies interacted in the varying political environments to determine the decisions that were made.

I found it troublesome that nowhere in the text is there a simple graph describing the numbers of Whooping Cranes extant in the wild and/or in captivity. Much of the data is mentioned in the text, but it does not appear to be complete and it is extremely difficult to locate. It is clear that there are presently many more Whooping Cranes than there were in, say 1954, but exactly how the various management techniques that have been applied relate to the number of birds is not.

There appears to have been only minimal editing done on the original manuscript and I found a large number of spelling errors and other typographic mistakes all over the book. Most of the time these were merely annoying, but when numbers were transposed in years, these mistakes were greatly misleading.

The strongest feature of this book is its 28-page bibliography. This contains essentially all of the relevant literature on Whooping Cranes and is a must for anyone who wishes to try writing the definitive history of Whooping Crane conservation in North America.—HERBERT T. HENDRICKSON.

A PASSION FOR BIRDS. AMERICAN ORNITHOLOGY AFTER AUDUBON. By Mark V. Barrow, Jr. Princeton University Press, Princeton, New Jersey. 1998: 326 pp., 33 unnumbered text figures. ISBN 0-691-04402-3. $39.50 (cloth).—Histories of ornithology, and especially of American ornithology are rare and those by professional historians of science are rarer still as shown by a perusal of the bibliography of this excellent new book by Mark Barrow. Barrow's *A Passion for Birds* does not provide such a complete history of North American ornithology as this was not his purpose in writing this particular analysis; ornithologists who are looking for a full history of their field may be disappointed, but should not be. Rather the goal of Barrow's book is to examine the rise of professionalization in ornithology from the death of Audubon in 1851 to 1940. It is a most excellent treatment of this important aspect of ornithology, one which is well worth the close attention of everyone interested in this biological discipline. *A Passion for Birds* is a superbly excellent history of science with full documentation and an exhaustive bibliography. Barrow chose to begin his analysis at 1850 because this coincides with Audubon's death in 1851 and continues Farber's analysis which ended in 1850. Barrow undertook a most intensive study of archives and the literature, as demonstrated by his citations, and presents a tremendous amount of information on the history of North American ornithology which is of interest to all ornithologists, professional and amateur alike. One does not have to be a historian of science to enjoy reading *A Passion for Birds* and to learn much from it.

Barrow stresses three topics in his analysis of professionalization of North American ornithology; these are: (a) collecting and systematics; (b) the American Ornithologists' Union founded in New York City in September, 1883; and (c) bird conservation. Quite clearly, the pathway for most early North Americans into ornithology, whether they remained amateurs or became professionals, was via the accumulation of a collection of bird skins or eggs.

Ornithology during the 19th century was characterized by intense activity amassing collections and describing the diversity of North American birds, first species and then subspecies, followed by those in the rest of the New World and finally the Old World. This descriptive work led to two different check-lists of North American birds, namely by Elliott Coues and by Robert Ridgway. It was largely the differences between these check-lists which led to the founding of the American Ornithologists' Union in 1883.

One of the important aspects in the professionalization of a science, as emphasized by Barrow, is the founding of a national society and the publication of a scholarly journal by that society. This was certainly true in the course of professionalization of ornithology in North America even if the initial goals of the American Ornithologists' Union were not quite so noble. Invitations were sent to a small group of ornithologists with the clear purpose of establishing a society with the primary goal of solving the check-list problem and with a structure which kept control of the society in the hands of a small group of leading ornithologists. The new Union solved splendidly the classification and nomenclature problems in short order, publishing the first edition of its check-list and its code of nomenclature in 1886. Professionalization was further achieved with the decision to accept the offer to take over the *Bulletin of the Nuttall Ornithological Club* as *The Auk*.

However, the AOU was less successful in dealing with other ornithological matters. The formal hierarchical structure of membership classes, designed to keep the large masses of amateur and other ornithologists out of the running of the Union, caused problems from the beginning which became more serious as the decades passed; this archaic system is still in place as the 20th century draws to a close. Moreover, the Union did not deal readily with other ornithological questions such as migration and bird protection, largely because of the preoccupation of the leading members with matters of collecting and systematics.

Barrow discusses in detail the development of conservation and bird protection which became a central issue for the Union from its origin. He showed that although several prominent members of the AOU had central roles in the development of bird protection in North America, the Union did little in this area. A large part of the problem stemmed from con-

flicts between member in favor of collecting birds for scientific (as opposed to commercial) purposes and those in favor of bird protection. Barrow does an excellent job in summarizing these arguments and showing their consequences for the Union and for conservation groups; but he fails to analyze these arguments and therefore does not show that these two groups were largely arguing past one another. By 1900, it was clear that collecting birds had nothing to do with the decline and extinction of avian species. Rather it was clear that the primary factors were market hunting and habitat destruction.

The second major aspect, and perhaps the more difficult one to analyze, in the professionalization of a science is the balance between amateurs and professionals. Barrow states (p. 5) that ornithology is "a classic example of an inclusive scientific field" but does not clarify this concept. He pays most careful attention to the professional–amateur distinction in his introduction providing numerous citations to the literature in this field, but does not come to a clear resolution because of the quandaries in defining an amateur (including whether a single definition would serve equally well in 1880, 1930, and 1980, and in characterizing particular persons as an amateur or as a professional. Was Sir William Herschel (1738–1822) an amateur astronomer when he discovered the planet Uranus in 1781, a time when he was still earning his keep as a musician? Were William Brewster, Elliott Coues, Margaret M. Nice, or Lord Walter Rothschild amateurs? Possibly this quandary will never be settled. Major questions still exist, such as: How much interest in ornithology does a person have to have to be identified as an amateur ornithologist? Is every person who maintains a bird feeding station and possesses a pair of binoculars and a bird identification guide, an amateur ornithologist? Perhaps a distinction should be made between serious amateur ornithologists and all others (the "hobby-ornithologists" as expressed in German). What were the roles of amateurs to ornithology since 1850? Since 1900? Since 1940, the end of Barrow's analysis? And is ornithology the science in which professionals are so outnumbered by amateurs (see statement by Frank Chapman, p. 5)? I think not. I suspect that ornithologists have over-emphasized the number and importance of amateurs in their science. Comparative studies are needed. But I suspect that there have been and still are more serious amateur astronomers than serious amateur ornithologists, and that these amateur astronomers have and continue to contribute more to astronomy than amateur ornithologists do to ornithology.

Nevertheless, Barrow was able to demonstrate that by 1940, the termination of his analysis, North American ornithology had become fully professionalized from its largely non-professional status in 1850. By 1940, a good majority of active ornithologists were professionals based on publishing scholarly works in avian biology and earning their living in a position requiring some involvement in the study and/or conservation of birds. Fifty years later, serious amateur ornithologists have all but disappeared. Clearly professionalization in ornithology and other sciences is dependent on the rise of paid positions in the field, but this aspect has not been examined for ornithology in any detail by Barrow or specifically mentioned in the end notes, possibly because it is too obvious. Yet, it would be most interesting to have a detailed analysis of the employment opportunities for North Americans in all aspects of avian biology from teaching and research to conservation and protection as well as the diversity of possibilities in government, publishing, and industry, as well as the changes in these employment opportunities over the decades.

I would like to congratulate Mark Barrow on his excellent analysis of the professionalization of North American ornithology and for presenting it in the clear and lively style used in *A Passion for Birds*. I thoroughly enjoyed reading this book and learned a great deal about the history of North American ornithology and the course of professionalization of a scientific field. Without any hesitation, I can recommend most firmly *A Passion for Birds* to everyone with any interest in ornithology. I would like to thank Keir B. Sterling for answering urgent questions on the fine points of American ornithology and for reading the manuscript.—WALTER J. BOCK.

THE EBCC ATLAS OF EUROPEAN BREEDING BIRDS: THEIR DISTRIBUTION AND ABUNDANCE. W. J. M. Hagemeijer and M. J. Blair (editors). T. and A. D. Poyser, London. 1997: cxli + 903 pp. $88.00.—Twenty-six years in the making, this book is a monumental work and one of the three most significant bird books to emerge from Europe in recent years. Weighing in at over six pounds (if my bathroom scales are correct), its 900-plus large format (8½″ × 12¼″) pages report on the distribution and relative abundance of birds across the European continent, ranging from Gibralter north to Ostend, and east to Svalbard and Novaya Zemlya and Franz Josef Land and south again to the eastern Mediterranean. Significant parts of Russia and the Ukraine are covered, as is Madeira and the Azores but the Mediterranean islands administered from North Africa, as well as Cyprus and the Canary Islands are omitted. In addition, an important part of the Western Palearctic, the North African coast, is also omitted. Within this area some 10,000 plus ornithologists from every European country obtained presence/absence data on some 495 species in over 4400 50 × 50 km^2, often with estimates of the order of magnitude of each population. Coverage is nevertheless regionally uneven, with large areas of former USSR countries lacking any data at all and with Norway, Poland, and parts of four western countries lacking the quantitative population estimates available for most countries. The area to be covered was only about half again as large as the conterminous United States and the number of countries (ca 40, depending on which year one considers) was about the same as the number of states in the U.S. but was complicated by the presence of about 40 different languages and the occasional armed conflict between countries! These political, language, and cultural differences meant that a large part of the success of the project depended on the use of relatively simple methods that could be adopted and implemented relatively rigorously by observers of diverse background.

The book is divided into two major sections, one of 141 (i–cxli) introductory pages, followed by 903 substantive pages. A Foreword by the eminent biogeographer K. H. Voous, a 3-page Preface, and an 8-page English language Introduction describe the purpose and structure of the Atlas. Figure 1 is particularly important in that it documents the completeness of coverage. I could find no quantitative figures as to the coverage achieved, but it looks as if about two-thirds of the squares received data for at least 75% of the breeding species expected to be found there. However, a large chunk of the former USSR received no data at all and there are also gaps in Albania and some of the outer island groups. The remaining squares, particularly concentrated in eastern Europe, received data for fewer than 75% of the breeding species anticipated. What could have been usefully included here is a political map of the region: country boundaries are shown but not identified, leaving readers unfamiliar with the political geography of Europe to guess which country is which.

The Atlas is mapped on a Universal Transverse Mercator (UTM) projection, chosen because it covered the intended area of the Atlas, was familiar in most European countries, and was compatible with national map projections for each country. Each UTM 100 km × 100 km square was subdivided into four smaller 50 × 50 km grid squares to parallel an earlier botanical Atlas. Because lines of longitude converge towards the poles, gradual reduction of the number of 50 × 50 km squares on northern lines of latitude was necessary. Despite this the visual effect on the final Atlas is very acceptable, with one having to look closely to find areas where the local density of dots was not regularly spaced.

Originally intended for 1985–1988, Atlas field work actually took far longer. Data for Spain, for example, spanned from 1970 to 1992, those from Finland and from Moldova spanned 1986–90, those from Georgia were for 1992, and the few species that were covered in Azerbaijan came from 1994. For some countries visitors' records contributed significantly to the information available. A standard form allowed recording the breeding status of about 440 species recorded for each square. Seven classes of information (e.g., distraction displaying, egg shells found, fledged young, nests seen) confirmed breeding, another of seven classes (e.g., pairs observed in suitable nesting habitat in the breeding season, courtship display observed, nest being seen, etc.)

indicates probable breeding, and two categories (species observed in possible nesting habitat in the breeding season, and seeing males present in breeding season) indicated possible breeding. The validity of the data was reviewed through a hierarchy of subsequent checking, ranging from EBCC national and regional coordinators through species experts to the authors of the species texts. In addition to the presence/absence data, the Atlas sought to include logarithmic population size estimates as semi-quantitative information of population levels. However, organizers in some countries (Norway and Poland) refused entirely to provide such estimates and small or large parts of several other countries (Iceland, France, Italy, Spain) likewise lack such estimates. Not surprisingly with armed conflict there "the project lost contact with Bosnia and Serbia, . . ." and had to make use of earlier presence/absence data from that region. Estimates from border squares between countries were merged to the higher value.

The main body of the Atlas consists of species accounts. Part 1 includes 496 species for which the mapping data were satisfactory in quality; a second group of 17 poorly covered species is covered in a series of briefer accounts. Each species account covers as far as possible a list of standard topics, including world distribution, breeding habitat, distribution and abundance in Europe, recent changes in status, and migration patterns. The accounts do not cover breeding biology and conservation status since these two topics are respectively covered in detail in the standard work on the region (Cramp *et al.*'s 1977–94 nine-volume *Birds of the Western Palearctic*) and in Tucker and Heath's (1994) *Birds in Europe—their conservation status*. The status of subspecies is referenced briefly in the species section. For each species a population size estimate is provided as the geometric mean of the population size in pairs, together with estimates of the minimum and maximum population, the year of the estimate, and the population trend in numbers and range size. Population change estimates cover five categories of decreases or increases of more than 50%, of 20–50%, and stable (± 20%).

The English introduction is followed by a translation of the introduction into thirteen languages, namely Czech, German, Castilian, French, Finnish, Greek, Hungarian, Italian, Dutch, Portuguese, Polish, Russian, and Swedish. Then follow two figures showing the maximum data quality and the minimum data quality for each square, for the best coverage and worst coverage species respectively. These are, in my view, rather uninformative figures, given the extreme nature of the outliers. A copy of the recording form then precedes a four page account of the project's organization and background. Reading between the lines, it is evident that two countries, Britain and the Netherlands, were the major drivers of the project, providing both initial funding and much in-kind support. Intriguingly, a significant amount of support came from a "sponsor a species" campaign in which individuals, organizations, and commercial firms undertook to sponsor the cost of analysis and writing-up species accounts. The 512 species required authors from 37 countries, typically involving people from two countries at opposite ends of the species range, thus promoting national collaboration and a broad perspective on the treatment of the species.

The remainder of the introductory material includes an 8-page account of the evolution and history of the European bird fauna by Jacques Blondel, an acknowledgments section, a bibliography of national and major regional bird books for Europe, and a 2-page introduction to the individual species accounts.

The Atlas maps and accompanying species accounts form the core of the volume. Each Atlas map contains insets for six island groups (Svalbard, Franz Josef Land, Novaya Zemlya, the Azores, the Madeiran archipelago, and the Selvagens). However, one is expected to memorize the identity of each of these insets, the only key being on page cxl. Within each map different colored dots distinguish unsurveyed squares from absence and mere presence from estimated abundance, and show whether breeding was confirmed or probable or merely possible. Dot size characterizes logarithmic abundance (1–9 breeding pairs, 10–99 pairs, etc., through "more than 100,000 breeding pairs"). For parts of Russia colored shading indicates extrapolation of presence from earlier literature was necessary. Most species accounts in Part 1 also include a graph and pie chart providing information on pop-

ulation size and trends in each of the major countries, a tally of the total number of European countries in which the species breeds, and an estimate of its European population (excluding Russia and Turkey). Most species accounts are illustrated by a black and white drawing of the species by a variety of European artists and each has a list of the species name in 14 European languages. The accounts for the 17 irregular or rare breeding species in Part 2 typically include an illustration and a short text commenting on its status.

The species accounts are followed by a short (5-page) account of the conservation status of European birds, adapted by Melanie Heath and Graham Tucker from their 1994 book *Birds in Europe—their conservation status*. A short summary provides an overview for the European avifauna as a whole. The remaining pages are essentially technical miscellania, with a 65-page bibliography and indices of scientific names and indices in the various languages of the book concluding the work.

There is an old joke in computer science to the effect that it pays to be first or third: if you are first, you get the credit; if you are third, you get something that actually works. This volume is undoubtedly in the first category. It provides an excellent approximation to a continent-wide atlas, and one that is infinitely superior to the range maps drawn by guesstimate in earlier regional or European avifauna and field identification guides. However, the differing effort afforded by different countries, the variation in timing of field work, the differing national perspectives as to the inclusion of population estimates, and the major uncertainties about the status of species within the former USSR, limit the scientific quality of this work. Nevertheless, the coverage of some 4400 50 × 50 km squares by a network of volunteer observers organized on essentially a shoestring budget is a stunning achievement. For a North American audience this work takes away any excuse for not having a Canada/United States/Mexico atlas of bird distributions, the major gap in our current spectrum of ornithological resources. For European biogeographers it creates a tremendous new database that will undoubtedly fuel innovative analyses of large-scale bird distributions on a scale previously impossible. And for a European Union that is increasingly moving to becoming a "United States of Europe" this work provides a remarkable conservation resource that should guide pan-European conservation strategies, at least for birds, over the next few decades. For ornithologists of all nationalities the book is a beautifully produced volume that will invite browsing, stimulate comparisons, and provoke thought for years to come—RAYMOND J. O'CONNOR.

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FRONTISPIECE. Left from top to bottom: *Myrmotherula haematonota haematonota* male, *Myrmotherula haematonota pyrrhonota* male, *Myrmotherula haematonota pyrrhonota* female, *Myrmotherula spodionota spodionota* male, *Myrmotherula spodionota spodionota* female. Right from top to bottom: *Myrmotherula fjeldsaai* male type, *Myrmotherula fjeldsaai* female, *Myrmotherula leucophthalma leucophthalma* male, *Myrmotherula leucophthalma leucophthalma* female. Water color painting by J. Fjeldså.

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A NEW SPECIES IN THE *MYRMOTHERULA HAEMATONOTA* SUPERSPECIES (AVES; THAMNOPHILIDAE) FROM THE WESTERN AMAZONIAN LOWLANDS OF ECUADOR AND PERU

NIELS KRABBE,[1,6,7] MORTON L. ISLER,[2] PHYLLIS R. ISLER,[2]
BRET M. WHITNEY,[3] JOSE ALVAREZ A.,[4] AND PAUL J. GREENFIELD[5]

ABSTRACT.—A new species of antwren (*Myrmotherula fjeldsaai*) closely related to *Myrmotherula haematonota* is described from the lower tropical zone of eastern Ecuador and immediately adjacent Peru. It primarily differs from *M. h. haematonota* by its brown instead of red back in both sexes. New distributional data for nominate *M. h. haematonota* shows that it meets the new species north of the Río Marañón, between the Ríos Napo and Pastaza, with no apparently significant physical barrier between them. *Received 6 March 1998, accepted 30 Dec. 1998.*

Two species of "stipple-throated" antwrens, Ornate Antwren (*Myrmotherula ornata*) and White-eyed Antwren (*Myrmotherula leucophthalma*) show distinct geographical variation in back color. In some populations of each species the back is rufous; in others it is gray or olive-brown. Separated by large rivers, these populations are not in physical contact and have traditionally been ranked as subspecies. Here we describe similar variation in *Myrmotherula haematonota,* but, because the two forms are known to be in contact and to retain their integrity, we propose to rank them as species.

Zimmer (1932) defined *Myrmotherula haematonota* to encompass both the rufous backed forms that occupy Amazonian lowlands and the gray backed forms of Andean foothills. He believed two specimens from the lowlands of Loreto, Peru, to be intermediate between these forms. More recently, Hilty and Brown (1986) and Parker and Remsen (1987) considered the foothill forms as a distinct species, *Myrmotherula spodionota* (including *sororia*), but did not address the issue of the apparently intermediate specimens.

METHODS

In 1992 PJG noticed a male specimen with a brown back in the collection of the Museo Ecuatoriano de Ciencias Naturales (MECN), labeled as *M. h. haematonota,* taken at Río Bufeo in the lowlands of Pastaza by R. Olalla on 3 February 1963. This specimen was referred to *Myrmotherula leucophthalma* by Ortiz-Crespo and coworkers (1990) and by Ridgely and Tudor (1994).

In 1994 NK tape recorded and collected a male and a female "stipple-throated" antwren with brown backs near Pompeya, Napo, Ecuador. These specimens and the Río Bufeo male were compared directly with the

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male from the "Mouth of Río Curaray" at the American Museum of Natural History (AMNH). The male is one of two specimens Zimmer (1932) identified as intermediate between the lowland and foothill forms. Six additional specimens of the brown backed form were later collected or located in the Western Foundation of Vertebrate Zoology (WFVZ), Louisiana State University, Museum of Zoology (LSUMZ), Museum of Natural History, University of Kansas (MNHUK), and Museo de Historia Natural de San Marcos (MUSM). Four records were available only as photographs. Thus, 12 specimens (4 of them photographic) were compared: 7 males and 5 females. All males were compared directly with the Río Curaray specimen. Two females were compared with each other by NK, three by MLI. Both red backed and brown backed forms were collected along Río Tigre, Loreto, Peru in 1995. An apparently intermediate specimen (not located) from an unspecified locality along Río Tigre was described as having the back "dark olive-brown, some of the feathers of the middle of the upper back with rufous brown edges" (Hellmayr 1910), suggesting some gene flow between the two forms. This was the second specimen that Zimmer (1932), without examining it, had considered intermediate between *M. h. haematonota* and *M. h. spodionota.*

RESULTS

Specimens of each sex of the brown backed birds were found to be essentially identical, suggesting a homogenous population rather than birds variously intermediate between *M. haematonota* and *M. spodionota.* The grayish edges of the inner webs of the remiges in the males (reddish in *M. leucophthalma*) and the coloration of the underparts of the female indicate that the brown backed specimens are more closely related to *M. haematonota* and *M. spodionota* than to *M. leucophthalma.* An analysis of vocalizations (unpubl. data) confirms this relationship. Nominate *M. h. haematonota* was found to be parapatric with brown backed birds in seemingly uniform habitat (see Fig. 1). Brown backed birds are uniform in plumage over a large area and thus clearly represent a valid taxon. They are replaced sharply by red-backed birds in similar habitat, suggesting species rank of the new taxon, which we propose to name:

Brown-backed Antwren *Myrmotherula fjeldsaai*, new species

Holotype.—MECN 6924, adult male obtained by N. Krabbe 16 July 1994 near Río Tiputini, 37 road km south-southwest of Pompeya, Provincia de Napo, Ecuador; 0° 38′ S 76° 26′ W, altitude 275 m. Blood sample (NK14-16.7.94) deposited at Zoological Museum, University of Copenhagen. Vocalization recordings (LNS 65998) archived at the Library of Natural Sounds, Cornell Laboratory of Ornithology.

Diagnosis.—Capitalized names and numbers of colors follow Munsell Soil Color Chart (Kollmorgen Instruments Corp., 1994 edition). Size, shape, plumage pattern, and coloration similar to those of *M. haematonota haematonota,* except that the mantle and back are between Dark Yellowish Brown (10YR3/4) and Dark Brown (10YR3/3). In *M. h. haematonota* the back is Dark Red (varying between 2.5YR4/8 and 2.5YR3/6). The male of *M. fjeldsaai* differs from *M. h. pyrrhonota* by having brown instead of red back, paler flanks and tail, and larger and pale buff instead of pure white spots on tips of median and some lesser coverts. Female differs from *M. h. pyrrhonota* by having a red back, pale (mostly white) throat streaked with black, and buffy brown breast and belly; in *M. h. pyrrhonota* the throat is yellow ochre and usually unstreaked, and the breast is reddish brown (Table 1). Male differs from *M. spodionota* by having a brown instead of pure gray back; larger, more buffy, and rounded wing covert spots, distinctly lighter gray underparts with darker olive brown sides and flanks, and by not showing the tendency in many individuals of *M. spodionota* to have the white streaks of the throat that continue onto the breast and sometimes even the belly. Female differs from *M. spodionota* by having a red back and being considerably paler throughout with whitish, black-streaked throat and virtually uniform buffy brown breast and belly. *Myrmotherula spodionota* has a somewhat flammulated yellow ochre throat, breast and belly (with throat lightly marked; Table 1). Females differ from the two known females of *M. h. haematonota* from north of the Río Marañón by throat color (Table 1), but this difference falls within the variation seen in large samples of *M. h. haematonota* and *M. h. amazonica. Myrmotherula fjeldsaai* differs from brown backed forms of *M. leucophthalma* by having darker general coloration and smaller, paler, and decidedly more rounded wing spots; male has grayish as opposed to buffy inner webs of remiges, and usually has smaller throat spots; female has

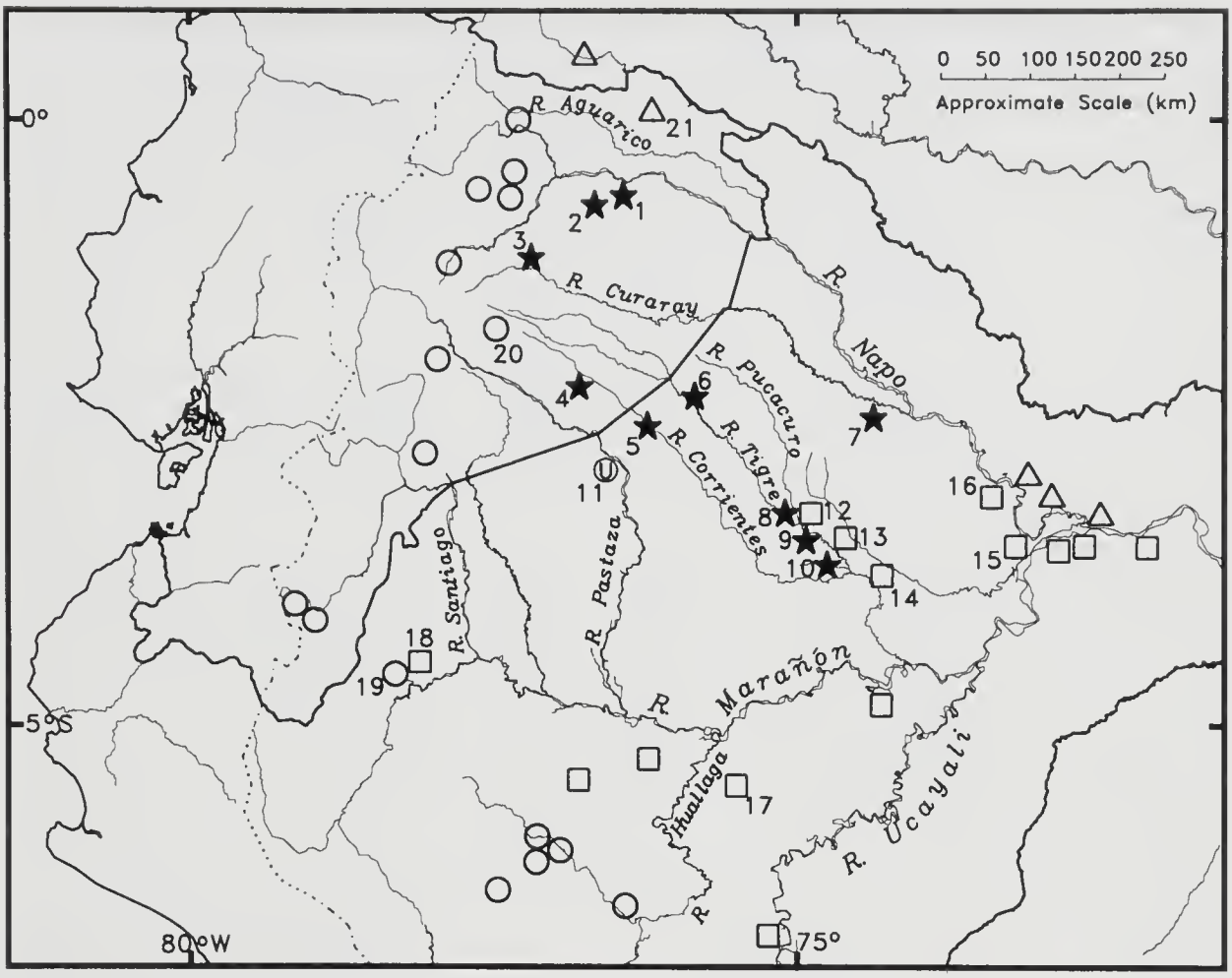

FIG. 1. Distribution of taxa of the *Myrmotherula [haematonota]* superspecies in the eastern Ecuador-northern Peru region. Heavy lines = coast and national boundaries. Dotted line = continental divide. Black stars = *Myrmotherula fjeldsaai.* Open circles = *M. spodionota* (including *sororia*). Open squares = *M. h. haematonota.* Open triangles = *M. h. pyrrhonota.* Circle surrounding a "U" = species unknown. Identification of locations discussed in text and type localities (identification of other locations on map available from MLI): 1. Río Tiputini (0° 38′ S, 76° 26′ W), Napo; type locality of *M. fjeldsaai.* 2. "Sunka 1" (0° 42′ S, 75° 51′ W), Napo. 3. Tzapino (ca 01° 11′ S, 77° 44′ W), Pastaza. 4. Río Bufeo (ca 02° 12′ S, 76° 48′ W), Pastaza. 5. Teniente Lopez (ca 02° 32′ S, 76° 14′ W), Loreto. 6. San Jacinto (ca 02° 21′ S, 75° 43′ W), Loreto. 7. Mouth of Río Curaray (ca 02° 24′ S, 74° 04′ W, exact location of collecting station uncertain), Loreto. 8. Cocha Hildalgo, left bank Río Tigre above mouth of Río Pacacuro, Loreto. 9. Vicinity of Intuto, right bank Río Tigre (03° 16′ S, 75° 04′ W), Loreto. 10. Río (Quebrada) Pavayacu, Loreto. 11. Andoas, Loreto. 12. Río Pacacuro, left bank near mouth, Loreto. 13. Santa Andrea, left bank Río Tigre approximately half way between mouth of Río Pacacuro and Intuto. 14. Nuevo Manchuria (03° 50′ S, 74° 19′ W) and Nuevo Tarma (03° 48′ S, 74° 21′ W), left bank Río Tigre, Loreto. 15. Puerto Indiana, Loreto. 16. Libertad, Loreto. 17. Chamicuros, Loreto; type locality of *M. h. haematonota.* 18. Huampami (200 m), Amazonas. 19. Río Kagka (800 m), Amazonas. 20. Sarayacu, Pastaza; type locality of *M. spodionota.* 21. Tigre Playa, Sucumbíos (MECN 6750 and 6751).

mottled cheeks, whitish-streaked throat and buffy brown breast, as opposed to uniform bright buffy yellow cheeks, throat and breast in *M. leucophthalma.*

Description of holotype.—Above, including most of crown, between Dark Yellowish Brown (10YR3/4) and Dark Brown (10YR3/3), edge of tail and 1–2 mm wide tips of feathers of back a more reddish Dark Brown (7.5YR3/3). Wing coverts brownish black with pale tips, forming three distinct rows of pale Reddish Yellow (7.5YR8/6) spots. Inner webs and basal half of outer web of inner greater secondary coverts Dark Brown (10YR3/3) to Dark Yellowish Brown (10YR3/4), inner webs washed with Dark Brown (7.5YR3/3) on their tips. Primary coverts blackish brown with minute, barely discernible, Reddish Yellow (7.5YR6/8) tips. Pale tips of the two alula feathers as large as on secondary coverts, but lighter, whitish on outer web. Median coverts and the largest of the

TABLE 1. Diagnosis of plumage differences of females of *Myrmotherula fjeldsaai* and neighboring populations in the *M. [haematonota]* superspecies.

	M. spodionota $n = >10$	*M. fjeldsaai* $n = 5$	*M. h. haematonota* from north of Rio Marañón; $n = 2$	*M. h. pyrrhonota* from north bank of Río Napo; $n = 2$
Chin & throat	Buffy Yellow to Yellow Ochre 10 YR8/6 to 10YR6/8	Mostly white; sides faintly tinged yellow brown	Pale Buff 10YR8/2	Buffy Yellow 10YR8/6 to Yellow Ochre between 10YR7/6 and 7.5YR7/6
Streaks on throat	Streaks are minimal, but blackish feather bases show through	Moderate to heavy blackish streaks over blackish feather bases	Moderate to heavy blackish streaks over blackish feather bases	Usually no streaks, sometimes a few fine streaks, but blackish feather bases not apparent
Center of breast to upper center of belly	Yellow Ochre 10YR7/6 to 10YR6/8 spots; lateral feather edges like sides giving a spotty appearance	Buffy Brown to Light Yellowish Brown 10YR7/4 to 10YR6/4 suffused with Light Olive Brown 2.5Y5/3	Buffy Brown to Light Yellowish Brown 10YR7/4 to 10YR6/4 suffused with Light Olive Brown 2.5Y5/3	Reddish-yellow 7.5YR6/8, suffused with Light Olive Brown 2.5Y5/3
Crown & anterior mantle	Very Dark Grayish Brown 2.5Y3/2	Dark Yellowish Brown between 10YR4/4 & 10YR4/6	Olive Brown 2.5Y4/3	Olive Brown 2.5Y4/3
Posterior mantle to tail coverts	Same as crown	Same as crown	Reddish Brown 2.5YR3/6 to 4/6 to Dark Reddish Brown 2.5YR4/8	Reddish Brown 2.5YR3/6 to 4/6 to Dark Reddish Brown 2.5YR4/8

lesser coverts blackish brown, spots palest on the distal coverts. The smallest of the lesser wing coverts mainly Bluish Gray (5PB5/1), each with a small, black bordered whitish dot at the tip. Forehead, cheeks, breast, and belly Bluish Gray (5PB5/1, but slightly lighter), flanks and vent between Olive Brown (2.5Y4/4) and Light Olive Brown (2.5Y5/4). Throat black, feathers with pale shafts and white tips, forming white, triangular spots pointing anteriorly. Inner webs of remiges gray. Twelve rectrices, tail strongly graduated, with tips of the three outer rectrices 16, 8 and 4.5 mm from the tips of the central pair of rectrices. Body mass 9.8 g. Irides grayish brown; bill blackish with thin gray blue line along cutting edge; feet gray blue. Skull 100% ossified. No Bursa Fabricii found. Largest testis 3 × 1 mm. No fat. Stomach contents: small arthropods (saved). Netted in tongue of flooded forest in hill country.

Variation in males.—Specimens from the Río Bufeo, the mouth of Río Curaray, and one hand held bird photographed near the type locality in 1994 (C. Canaday photo) were examined by NK and found to be similar to the type. The two old specimens were slightly lighter gray, equivalent to the difference seen between old and fresh material of *M. spodionota*. MLI made the same conclusions when he compared the Río Curaray specimen to the Teniente Lopez specimen and to the description of the Río Tigre specimen collected by JA. The backs of the males were slightly brighter (Dark Yellowish Brown, 10YR3/4) than the description of the type specimen; backs of two specimens were more Olive Brown (between 10YR3/4 and 2.5Y4/4); and all lacked the reddish brown feather tips described for the type specimen.

Additional male specimens examined.—*Myrmotherula fjeldsaai*: ECUADOR: Napo, Río Bufeo (MECN 2181). PERU: Loreto, mouth of Río Curaray (AMNH 255780); Ten-

iente López, Río Corrientes (MNHUK uncatalogued, skull incompletely ossified, collected July 1993 by Aucca); above Intuto, Río Tigre (collected January 1995 by JA, to be deposited in MUSM). *Myrmotherula h. haematonota* and *M. h. amazonica* (Museum abbreviations are followed by number of specimens): PERU: Loreto, Lores, Río Tigre (collected January 1995 by JA, to be deposited in MUSM, 2); Libertad, S bank Napo (LSUMZ, 2); Puerto Indiana, N bank Amazon (AMNH, 1); Quebrada Vainilla, S bank Amazon (LSUMZ, 5); Orosa (AMNH, 3); Sarayacu (AMNH, 2); 15 km E Puerto Maldonado (MNHUK, 1). BOLIVIA: (LSUMZ, 5). BRAZIL: (AMNH, 10). *Myrmotherula h. pyrrhonota*: ECUADOR: Sucumbíos, about 14 km N Tigre Playa (MECN, 1). PERU: Loreto, N of Río Napo, 157 km by river NNE of Iquitos (LSUMZ, 2); Río Yanayacu (LSUMZ, 2); Quebrada Orán (LSUMZ, 2). COLOMBIA: (AMNH, 1). BRAZIL: (AMNH, 8; USNM, 10). VENEZUELA: (AMNH, 26; USNM, 6). *Myrmotherula spodionota* including *sororia*: ECUADOR: Napo, San José Abajo (AMNH, 5; USNM, 1); above San José (ANSP, 1); Avila (ANSP, 1); above Avila (AMNH, 4); Chonta Urcu (ANSP, 1); Morona-Santiago, Cutucú (AMNH, 1). PERU: (AMNH, 8; LSUMZ, 23).

Female.—A topotypical young female (MECN 6925) with 2% ossified skull is similar to the male above, but slightly lighter and yellower (between 10YR4/4 and 10YR4/6), with tail feathers having Strong Brown (7.5YR4/6) lateral edges. Sides of head like crown, but with ill-defined buff mottling. Below Light Yellowish Brown (between 2.5Y6/4 and 10YR6/4), somewhat browner on sides and flanks, breast with faint pale flammulations. Throat white tinged Pale Yellow (2.5Y8/3), irregularly but conspicuously streaked by black edges (but not tips) on some feathers. Irides gray brown, bill like the type, feet slaty; body mass 9.0 g.

Another female netted and released at the type locality in 1994 by NK was similar, but with whitish irides and with narrower black edges on the feathers of the whitish throat; body mass 10.7 g. A third individual netted and photographed near the type locality in 1994 (C. Canaday photo) was found by NK to be similar. It had a whitish throat with narrow dark feather edges, appeared to have a fully ossified skull, brown irides, and blue gray feet; body mass 9.5 g. The foregoing description of MECN 6925 was found by MLI to match females taken at "Sunka 1", Tzapino, and San Jacinto, as well as the description and photographs of the specimen collected upstream from Intuto on the Río Tigre by JA, except that central feathers of throats were white (untinged) and lateral edges of tail feathers were the same as the color of the back (rather than reddish brown).

Additional female specimens examined.—*Myrmotherula fjeldsaai*: ECUADOR: Napo, "Sunka 1", 40 km S Coca (WFVZ 45662, collected November 1988). Pastaza, Tzapino (LSUMZ 83109, collected in May 1976 by Tallman). PERU: Loreto, San Jacinto, upper Río Tigre (MNHUK uncatalogued; collected in July 1993 by Aucca); above Intuto, Río Tigre (taken by JA in January 1995 and to be deposited at MHNJP). *Myrmotherula h. haematonota* and *M. h. amazonica*: PERU: Loreto, Libertad, S bank Napo (LSUMZ, 2); Puerto Indiana, N bank Amazon (AMNH, 1); the vicinity of Huampami, Amazonas, Peru, about 200 m elevation (LSUMZ, 1); Quebrada Vainilla, S bank Amazon (LSUMZ, 6); Orosa (AMNH, 1); Sarayacu (AMNH, 1); "mouth of Río Urubamba" (AMNH, 1). Madre del Dios, 15 km E Puerto Maldonado (MNHUK, 1). BOLIVIA: (LSUMZ, 5). BRAZIL: (AMNH, 7). *Myrmotherula h. pyrrhonota*: ECUADOR: Sucumbíos, about 14 km N Tigre Playa (MECN, 1). PERU: Loreto, Quebrada Orán (LSUMZ, 1). COLOMBIA: (AMNH, 1). BRAZIL: (AMNH, 16; USNM, 7). VENEZUELA: (AMNH, 26; USNM, 5). *Myrmotherula spodionota* including *sororia*: ECUADOR: Napo, San José Abajo (AMNH, 2; USNM, 1); Morona-Santiago: Chiguaza, Cutucú (ANSP, 1); Zamora-Chinchipe: Zamora (AMNH, 1). PERU: (AMNH, 4; LSUMZ, 20).

Mensural variation.—Measurements are given in Table 2. As a whole, measurements of populations in *M. haematonota* and *M. spodionota* do not differ significantly (Table 2). The only measurement whose ranges do not overlap are the wing measurements for the few known specimens of *M. h. haematonota* from north of the Amazon and *M. spodionota,* although there is only slight overlap of some wing and tail measurements of *M. spodionota* compared to other populations. Using a rule

TABLE 2. Measurements of six populations in the *Myrmotherula [haematonota]* superspecies. Sexes are combined. Bill is measured from the anterior nostril; wing is unflattened wing chord.

Measurement	*M. fjeldsaai*	*M. h. haematonota* north of Amazon	*M. h. haematonota* south of Amazon	*M. h. pyrrhonota* Venezuela & northern Brazil	*M. spodionota*
Bill Width	$n = 7$	$n = 6$	$n = 8$	$n = 10$	$n = 10$
Range	3.6–4.0	3.2–4.0	3.5–4.1	3.7–4.2	3.6–3.9
Mean ± SD	3.79 ± 0.14	3.58 ± 0.34	3.86 ± 0.18	4.05 ± 0.18	3.75 ± 0.13
Bill Depth	$n = 7$	$n = 6$	$n = 8$	$n = 10$	$n = 10$
Range	3.6–3.9	3.6–4.2	3.8–4.4	3.6–4.4	3.8–4.3
Mean ± SD	3.72 ± 0.15	3.83 ± 0.22	4.04 ± 0.21	4.03 ± 0.23	4.09 ± 0.19
Bill Length	$n = 10$	$n = 7$	$n = 10$	$n = 10$	$n = 10$
Range	8.4–9.5	8.3–8.9	8.4–9.6	8.8–9.7	8.2–9.4
Mean ± SD	8.97 ± 0.32	8.57 ± 0.30	9.07 ± 0.36	9.19 ± 0.31	8.81 ± 0.43
Tarsus Length	$n = 8$	$n = 6$	$n = 8$	$n = 10$	$n = 10$
Range	15–16	16–17	15–17	16–17	16–18
Mean ± SD	15.7 ± 0.5	16.2 ± 0.4	15.9 ± 0.6	16.1 ± 0.3	16.8 ± 0.6
Tail Length	$n = 10$	$n = 7$	$n = 10$	$n = 10$	$n = 10$
Range	33–39	34–37	34–39	34–38	37–40
Mean ± SD	35.8 ± 1.5	35.3 ± 1.1	35.1 ± 1.8	35.9 ± 1.3	38.4 ± 1.2
Wing Chord	$n = 10$	$n = 7$	$n = 10$	$n = 10$	$n = 10$
Range	47–54	47–50	48–53	47–51	51–55
Mean ± SD	49.8 ± 1.9	48.1 ± 1.1	50.3 ± 1.6	49.2 ± 1.4	52.6 ± 1.4

similar to one proposed by Amadon (1949), comparing means of measurements plus or minus three standard deviations, differences between wing and tail measurements of *M. spodionota* compared with *M. h. haematonota* north of the Amazon again stand out. Another, larger set of measurements (mean followed by range) confirms this tendency: the wing (53.8 mm; 51–56) and tail (38.9 mm; 33–43) measurements of *M. spodionota* ($n = 29$) compares to wing (51.0 mm; 46–54) and tail (36.4; 33–41) for all populations of *M. h. pyrrhonota* ($n = 86$) and wing (52.4 mm; 50–56) and tail (38.9 mm; 33–43) for all populations of *M. h. haematonota* ($n = 40$). Differences in bill among these larger samples were found to be insignificant.

Distribution.—South and west of the Río Napo in the lowlands of eastern Ecuador and extreme northern Peru. Geographic range extends from the type locality and from nearby "Sunka 1" in Napo, Ecuador, south to the central portion of the Río Tigre, a short distance upriver from Intuto, Loreto, Peru, approximately 360 km south-south-east of the type locality (Fig. 1). A sight record (Willis 1988) from Andoas, Loreto, may also be of this species.

Habitat.—At the type locality NK observed *M. fjeldsaai* in tangled, but fairly open understory to lower canopy in humid primary terra firma forest and into adjacent tongues of varzea forest. Near Sachacocha in the middle Río Tigre, Loreto, Peru, BMW and JA found *M. fjeldsaai* in tall, closed canopy (except for scattered treefalls), terra firme forest with an abundance of palms in the understory. Known from about 150 to 300 m elevation.

Vocalizations.—The loudsongs (Isler et al. 1998) of nominate *M. haematonota, M. fjeldsaai,* and *M. spodionota* (Fig. 2) are similar, but easily distinguishable from those of *M. leucophthalma* (Isler, Isler, and Whitney, unpubl. data). We do not provide a detailed analysis of differences among the loudsongs illustrated in Fig. 2 because the sample size for *M. fjeldsaai* is inadequate. However, pace (notes per sec), an element that appears to vary among the loudsongs of *M. haematonota* complex, has been shown to be one of the most important characteristics distinguishing loudsongs of closely related and syntopic pairs of Thamnophilidae (Isler et al. 1998).

Behavior.—Foraging behavior (NK, BMW, JA, C. Canaday, G. Rivadaneira, and R. S. Ridgely, unpubl. data), of *M. fjeldsaai* appears to resemble the other dead leaf specialists in the group as described by Gradwohl and Greenberg (1984), Rosenberg (1990, 1993, 1997), and Whitney (1994).

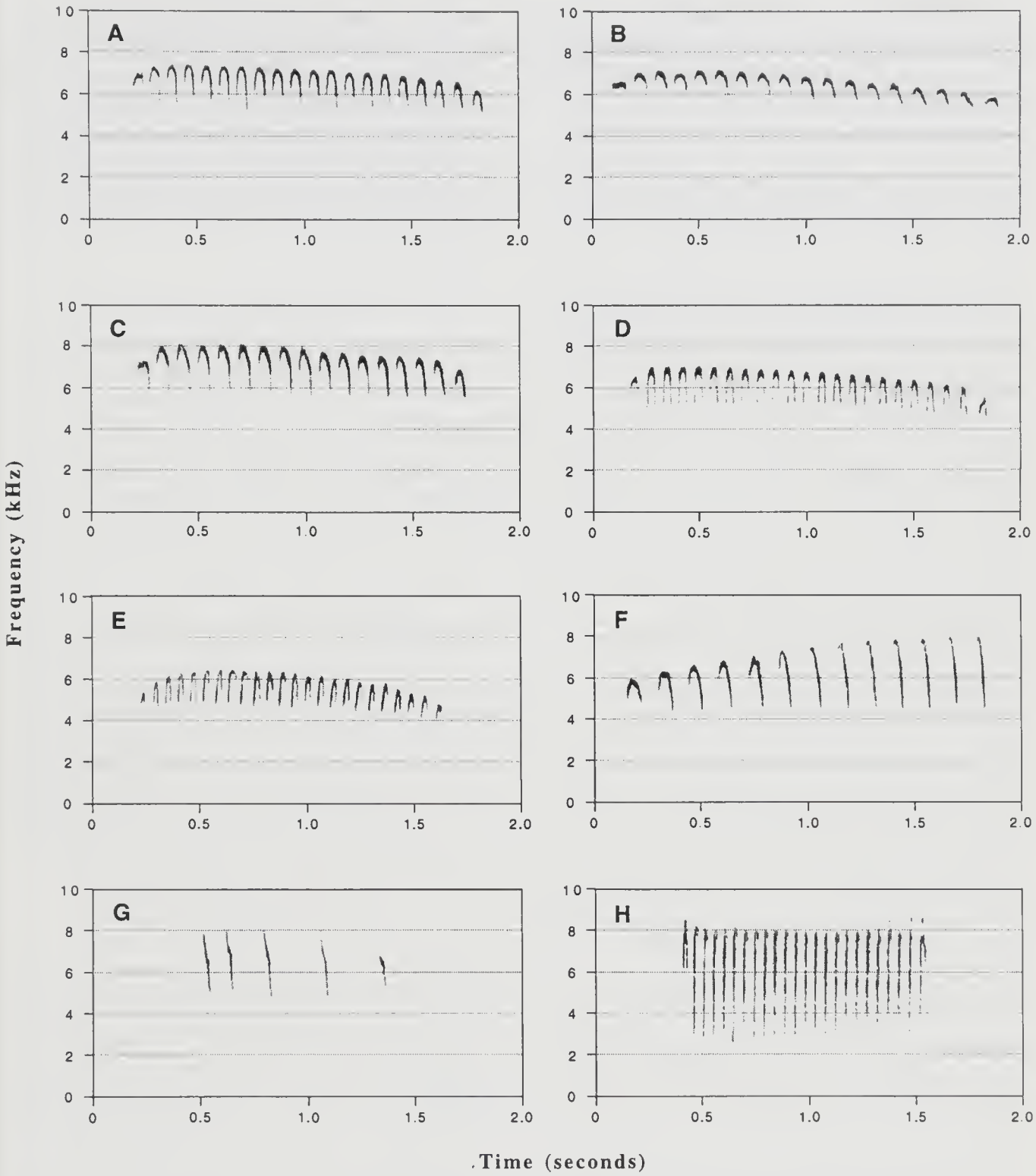

FIG. 2. Vocalizations of *Myrmotherula fjeldsaai* and loudsongs representative of neighboring populations of other taxa in the *M. [haematonota]* superspecies. A. *Myrmotherula fjeldsaai* loudsong from the type locality (recorded by N. Krabbe; LNS 65998). B. *Myrmotherula fjeldsaai* loudsong from Sachacocha, Loreto, Peru (B. M. Whitney; to be archived at LNS). C. *Myrmotherula h. pyrrhonota* loudsong from Quebrada Sucusari, Loreto, Peru (T. A. Parker, III; LNS 33798). D. *Myrmotherula h. haematonota* loudsong from Lores, Loreto, Peru (B. M. Whitney; to be archived at LNS). E. *Myrmotherula s. spodionota* loudsong from 30 km west of Loreto, Napo, Ecuador (B. M. Whitney; to be archived at LNS). F., G., and H. *Myrmotherula fjeldsaai* calls and rattle from the type locality (N. Krabbe; LNS 65998)—compare with the rattle of *M. spodionota* presented by Whitney (1994, fig. 1).

Taxonomic rank.—The possibility that *M. fjeldsaai* and *M. haematonota* occasionally hybridize is raised by the Río Tigre specimen described by Hellmayr (1910). However, the fact that the two maintain their integrity, despite being in contact in an area with extensive floodplain dynamics, makes it most probable that they are correctly ranked as full species.

Speciation.—In addition to being parapatric with *M. h. haematonota, M. fjeldsaai* might meet with *M. h. pyrrhonota* and *M. spodionota,* but there is no evidence of intergradation. To the southeast (Fig. 1) the ranges of *M. fjeldsaai* and *M. h. pyrrhonota* appear to be separated by the middle Río Napo, but both may occur farther upstream where the rivers Napo and Aguarico are narrow enough for them to cross. To the west, the ranges of *M. fjeldsaai* and *M. spodionota* appear to be separated altitudinally, with a narrow elevational band that neither species occupies. Neither was among the 505 species recorded at Jatunsacha, at 450 m during 26 months of field work (B. Bocham, unpubl. data). Nor has BMW found either between 400–600 m during extensive field work around the village of Loreto, Napo, Ecuador. Additionally, neither was among the six species of *Myrmotherula* recorded by NK during 12 days of field work at Canelos, Pastaza, 500–700 m. Because the forest is continuous between their elevational limits, further field work might show the two species' ranges to be in contact.

Conservation.—The known range of *Myrmotherula fjeldsaai* encompasses the Yasuni National Park (7281 km^2) in Ecuador (whence comes the type). Given that this huge area remains effectively protected, *M. fjeldsaai* appears not to be at risk at present.

Etymology.—We take the pleasure of naming this species in honor of Prof. Jon Fjeldså of the Zoological Museum, University of Copenhagen. Through his countless publications, most based on results obtained during field trips to the most hostile of environments, he has inspired a large number of biologists to leave their desks and get into the field. Among his achievements should also be mentioned his most recent work (with C. Rahbek) in delimiting areas of top priority for conservation in South America and Africa, work that could eventually save a number of species from extinction. Apart from his impressive professional knowledge and self discipline, his many achievements were possible only through his great understanding of human nature, his generosity and helpfulness, and his unfailing habit of treating everybody as an equal, legendary from the jungles of South America to Africa. The English name refers to the distinctive color of the back.

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COMPARATIVE SPRING HABITAT AND FOOD USE BY TWO ARCTIC NESTING GEESE

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ABSTRACT.—The timing of egg laying is generally constrained by female condition, which is partly determined by the food available to her before laying. Although it was generally believed that geese rely exclusively on internal nutrient reserves for egg production, spring feeding is intensive in many populations of geese, significantly adding nutrients necessary for egg production and incubation. We compared the spring feeding ecology of Greater White-fronted Geese (*Anser albifrons frontalis*) and Canada Geese (*Branta canadensis hutchinsii*) on a shared nesting ground on the Kent Peninsula, NWT (68° N, 108° W), where pairs feed intensively from arrival until incubation. Live plant biomass did not significantly increase within specific habitats during preincubation, but the total available biomass was greater after snow melt because habitats with higher biomass became available. Live plant biomass available in pond margins (30–60 g/m^2) was 4–15 times higher than in habitats that were available earlier, i.e., mud-flats and hummocks (4–8 g/m^2). Before snow melt, both species shared the 1–20% of the study area that was snow free (max. density 600 pairs/km^2), opportunistically used the only two available habitats, mud-flats and hummocks, and primarily ate (50–70%) tillers of *Puccinellia* spp. During snow melt, pairs dispersed, pair density decreased (max. of 40 pairs/km^2), and interspecific differences in habitat and food use appeared. White-fronted Geese used pond margins and ponds more often than Canada Geese. After snow melt, White-fronted Geese predominantly fed in ponds on *Carex* spp. and *Dupontia fisheri* rhizomes and basal stems; Canada Geese continued feeding opportunistically, pecking leaves in all habitats and grubbing rhizomes in pond margins and ponds. White-fronted Geese used the grubbing technique more often than Canada Geese in all habitats and periods. *Received 13 Feb. 1998, accepted 17 Nov. 1998.*

Energy investment by females in reproduction is highest during the period of egg formation in birds with precocial young, such as geese (King 1973). Clutch size and timing of laying are potentially constrained by female condition, which is partly determined by the amount of energy and nutrients available to her before egg formation (Drent and Daan 1980, Winkler and Walters 1983).

Early nesting is critical for Arctic nesting geese because of the short summer and the rapid seasonal decline in components of reproductive success such as gosling growth and probability of producing recruits (Barry 1962, Cooke et al. 1984, Cooch et al. 1991, Sedinger and Flint 1991, Lindholm et al. 1994). One strategy to facilitate early nesting is to carry nutrient reserves accumulated during migration to the breeding grounds (Ankney and MacInnes 1978, Wypkema and Ankney 1979, Ankney 1984, Budeau et al. 1991, Bromley and Jarvis 1993, Choinière and Gauthier 1995). There is, however, an upper limit to the amount of reserves that can be economically carried during migration (Lindstrom and Alerstam 1992).

In migratory birds, the timing of rapid follicular development (RFD) initiation with respect to spring migration may affect the relative contribution to egg production of nutrients acquired en route versus those acquired on nesting grounds. Timing of RFD initiation directly determines laying date of the first egg (reviewed by Rohwer 1992). Because some female geese in some locations typically nest soon (3–6 days) after their arrival on the nesting ground (*Anser rossii*: Ryder 1970; *Anser caerulescens caerulescens*: Ankney 1977, Ankney and MacInnes 1978; *Anser canagica*: Thompson and Raveling 1987; *Branta bernicla bernicla*: Spaans et al. 1993), RFD is initiated before arrival, hence the date of nest initiation is independent of food availability on the nesting ground (Raveling 1978, Ankney 1984, Newton 1977; but see Prop and de Vries 1993).

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In other populations most female geese lay at least 12 days after arrival on the nesting grounds, long enough for the completion of RFD of the first egg [*Branta bernicla nigricans*: Raveling 1978; *B. canadensis*: MacInnes et al. 1974, Bromley 1984; *A. albifrons*: Fox and Madsen 1981, Budeau et al. 1991; *A. caerulescens caerulescens* (at La Pérouse Bay): Findlay and Cooke 1982; *A. c. atlantica*: Gauthier and Tardif 1991]. In this case, food availability on the nesting ground can affect the date of RFD initiation, the date of nest initiation, and potentially clutch size and constancy of incubation. Most of the energy necessary for egg formation and laying was met by food on the nesting grounds for *A. albifrons frontalis* (Budeau et al. 1991), *B. canadensis occidentalis* (Bromley and Jarvis 1993), and *A. caerulescens atlantica* (Choinière and Gauthier 1995). Intermediate cases may occur where the time available for feeding between arrival on the nesting ground and laying varies greatly among females and/or among years within populations (Raveling 1978).

Food availability in the Arctic in spring was traditionally thought to be so low that, although female geese could feed, they could not meet their energy requirements for daily maintenance or egg production (Barry 1962, Ryder 1970; reviewed by Rohwer 1992). For some species, body mass of females generally increases before or during egg production (Wypkema and Ankney 1979, Budeau et al. 1991, Bromley and Jarvis 1993, Choinière and Gauthier 1995) indicating that energy intake during these periods could at least meet requirements for daily maintenance (Ganter and Cooke 1996, Carrière 1996). Further, variation in timing of nesting can be related to variation in food availability prior to egg formation (Prop and de Vries 1993). Thus, food availability and use in the Arctic in spring clearly is significant.

In the Arctic, food availability during preincubation is highly variable. This variation hinders interspecific comparisons of feeding ecology during preincubation because we cannot differentiate between factors that are site specific (e.g., weather, snow melt patterns, plant phenology) and species specific (e.g., body size, bill morphology; Prevett et al. 1985, Fox et al. 1992).

We compared the feeding ecology of Greater White-fronted Geese (*Anser albifrons frontalis*) and Canada Geese (*Branta canadensis hutchinsii*) during preincubation. These species have similar body mass (White-fronted Goose 8% > Canada Goose; R.G.B., unpubl. data), reproductive chronology, and share the same Arctic spring feeding and nesting grounds on the Kent Peninsula, NWT, Canada.

Our objectives were to determine (1) how snow melt affected the availability of feeding habitats and plant biomass, (2) whether White-fronted and Canada geese differed in their use of habitat and food during preincubation on a shared nesting ground, and (3) how changes in habitat and food availability resulting from snow melt affected dispersal, habitat and food use, and the timing of nesting in these two species of geese.

STUDY AREA AND METHODS

The study was conducted on the Walker Bay Study Area (68° 22′ N, 108° 04′ W), southwest Kent Peninsula, Northwest Territories (Fig. 1), as part of longterm studies on the breeding ecology of White-fronted and Canada geese (see Bromley et al. 1995). The shallow plain of the river valley is a high density nesting area for both species of geese (Bromley et al. 1995).

Studies of the feeding ecology during preincubation were made on an intensive study area positioned to permit semicontinuous observation of geese in spring while minimizing disturbance caused by human movements (Fig. 1). The area was further divided into two sites: site A (0.72 km^2) was representative of the habitats found all along the river and typical of areas in which arriving geese concentrated until snow melt; site B (4.33 km^2) was representative of the rest of the general study area where nesting typically occurred. Site A, a raised levee paralleling the river, was drier than site B. Habitats available to geese were classified from dry to wet: hummock, mud-flat, pond margin, and pond (see plant list per habitat in Carrière 1996). Mud-flat habitats were sparsely vegetated flats of exposed glacial marine sediments (ca 3000 yrs ago; Dyke and Dredge 1989), largely saline clays and silts. Hummock habitats were formed by frost heaves (5–30 cm high) and covered by thin soil where *Salix* spp. dominated. Pond margins were the edges of depressions that were wet from snow melt to early June, had low salinity, and formed meadows dominated by graminoids and forbs. Pond habitats were depressions 0.10–1.00 m deep, inundated at least until early July, and dominated by hydrophilic forbs. All habitats formed a fine grained mosaic with patches (i.e., continuous areas of same habitat) of various shapes. Most patches covered 50–900 m^2, with some mud-flats outside sites A and B extending more than 1 km^2.

General phenology.—We recorded the phenology of

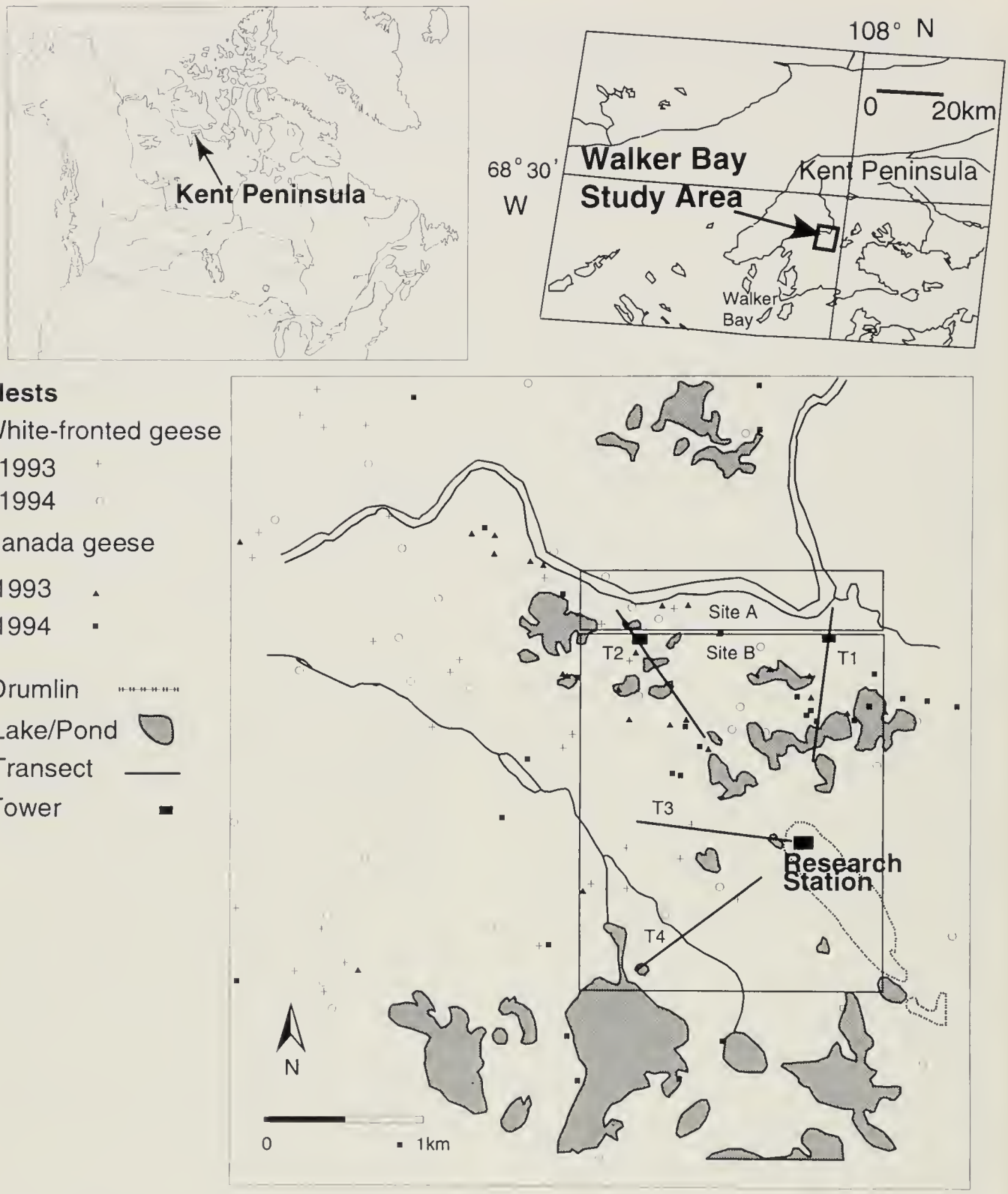

FIG. 1. Walker Bay Study Area is situated in a valley near Walker Bay on the Kent Peninsula, NWT, Canada. A section selected for detailed study was divided into 2 sites: site A was snow-free first in spring and was typical of habitats available along the river banks. Snow melt phenology in site B was typical of the rest of the study area.

snow melt, goose arrival, and goose dispersal along four 1 km transects (Fig. 1). At 2–3 day intervals we visually estimated snow cover (±5%) in 200 × 200 m areas, situated in pairs, one on each side of the transect at each of five stations 200 m apart. Thus, we covered 11% of site A (2 stations) and 7% of site B (18 stations). At each station, we used binoculars to count and locate all geese that could be identified to species.

Preincubation was divided into three periods defined by snow melt phenology on site A: (1) before snow

melt (snow cover >80%), (2) during snow melt (snow cover = 20–80%)—a period of rapid change, and (3) after snow melt (snow cover <20%).

Nesting phenology.—Nests were located by observing nest building behavior from towers. Date of the first egg laid (i.e., date of nest initiation) was estimated only for nests found during laying by subtracting 1.3 d per egg (R.G.B., unpubl. data) already laid. Nests outside site A and B were located during ground surveys of randomly selected 1 km^2 plots (Bromley et al. 1995). We compared median laying dates for combinations of years and species using Kruskal-Wallis ANOVA on Ranks tests, followed by non-parametric multiple comparison tests using Excel 97 following Daniel (1978).

Habitat availability.—We measured habitat availability in the areas at two towers (see below) by mapping habitat patches with a 20 × 20 m grid in the field and using aerial photographs. Availability of a habitat was defined by the cumulative area of all patches of that habitat as a proportion of the total snow-free area. Only snow-free areas were considered accessible to feeding geese (Hall et al. 1997).

Use and selection of habitats.—We observed goose pairs throughout preincubation from two towers in 1993 and one tower in 1994. Daily observations were conducted from one tower at a time depending on the distribution of geese in the study area. We used the scan sampling method (Altman 1974), with scans conducted every 2–6 hr during the 24 hr cycle. During a scan, we observed all pairs present within 400 m of the observation tower. Sections of sites A and B were visible from both towers (Fig. 1). For each pair, we noted sex, behavior, and habitat used by each pair member. Sex was determined using relative neck size (larger in males), abdominal profile (larger in females with developing follicles; Owen 1981, Fox et al. 1995), and alert position (male usually standing higher). Pairs were recorded as feeding when either the female or both members were grubbing (on below-ground plant parts), pecking (on above-ground plant parts), searching for food (moving with head down), or drinking.

We calculated habitat use for each scan as the proportion of observed feeding pairs using each available habitat. Pond and pond margin use data were pooled as wet habitats to obtain sufficiently large samples for a *G*-test (Sokal and Rohlf 1981). For analysis, we pooled habitat use data within snow melt period and tower. Habitat use data were assumed to be independent within and between scans. This seemed reasonable for two reasons. First, preliminary observations on focal individuals indicated that pairs showed little synchronization in movements between habitat patches (i.e., no group behavior). Second, because of the extreme patchiness of habitats, pairs could use all available habitats within 2 hr (minimum time interval between scans); 58% of Canada Geese (n = 96) and 43% of White-fronted Geese (n = 69) individuals observed in focals used more than 1 habitat patch within 10 min (S.C., unpubl. data). The constant movement of pairs between the observed and unobserved areas during preincubation minimized pseudoreplication. For example, no individual with a coded neck collar (from 1987–1994 banding operations; Bromley et al. 1995) was observed in more than six different scans (only 30% of collared individuals were observed more than twice).

For each year and period, interspecific differences in habitat use were analyzed without reference to habitat availability using *G*-tests of independence, followed, when significant differences were detected, by pairwise unplanned comparison tests (Sokal and Rohlf 1981; using Excel 97).

Habitat use was compared to availability before and after snow melt, but not during melting, because availability changed too rapidly, i.e., from 20% to 80% snow-free area in <7 d. We used χ^2 goodness-of-fit tests, followed by Bonferroni simultaneous confidence interval tests (Sokal and Rohlf 1981, Neu et al. 1974; using Excel 97) to detect sources of significant differences (design 1 in Thomas and Taylor 1990).

Plant availability within habitats.—We estimated food plant availability in snow-free habitats by sampling randomly 20 × 20 cm quadrats within habitat patches in site A and B, 4 times between 17 May–14 June throughout preincubation (1993: n = 120; 1994: n = 218). We collected all above and below ground vegetation 0.1–3 cm deep then froze each sample for transportation. Ground vegetation below 3 cm was never thawed and was considered unavailable to geese. In the laboratory, live above and below ground vegetation was sorted by species, dried at 45° C to constant mass, and weighed. We pooled plant species according to food plant categories used in the analysis of feces (see below). Availability of each food plant category in each habitat was defined as the average proportion of total dry biomass represented by that category in each habitat during each snow melt period (Fig. 2).

We analyzed total (pooled species) above and below ground biomass separately. We first analyzed differences in total biomass among habitats and sampling dates for each year separately using Kruskal-Wallis ANOVA on Ranks tests, followed by multiple comparison tests to detect pairwise differences (Daniel 1978). We then pooled sampling dates and analyzed differences in biomass among habitats and years with Two Way ANOVA using square-root transformed data (Sokal and Rohlf 1981).

Diet.—We determined diet using two complementary methods: (1) microhistological analyses of feces and (2) detailed observations of feeding techniques. Additional data were available from the esophageal content of 16 female Canada Geese collected in 1994.

Throughout preincubation, we collected all feces that we could assign to an individual bird (i.e., a bird that was observed defecating). Feces were individually frozen for transportation, dried in the laboratory, and analyzed using microhistological techniques (see Johnson 1982). We sampled four slides per feces, with 20 observation fields per slide. We identified most plant fragments (80–100% per feces) to genus. We grouped

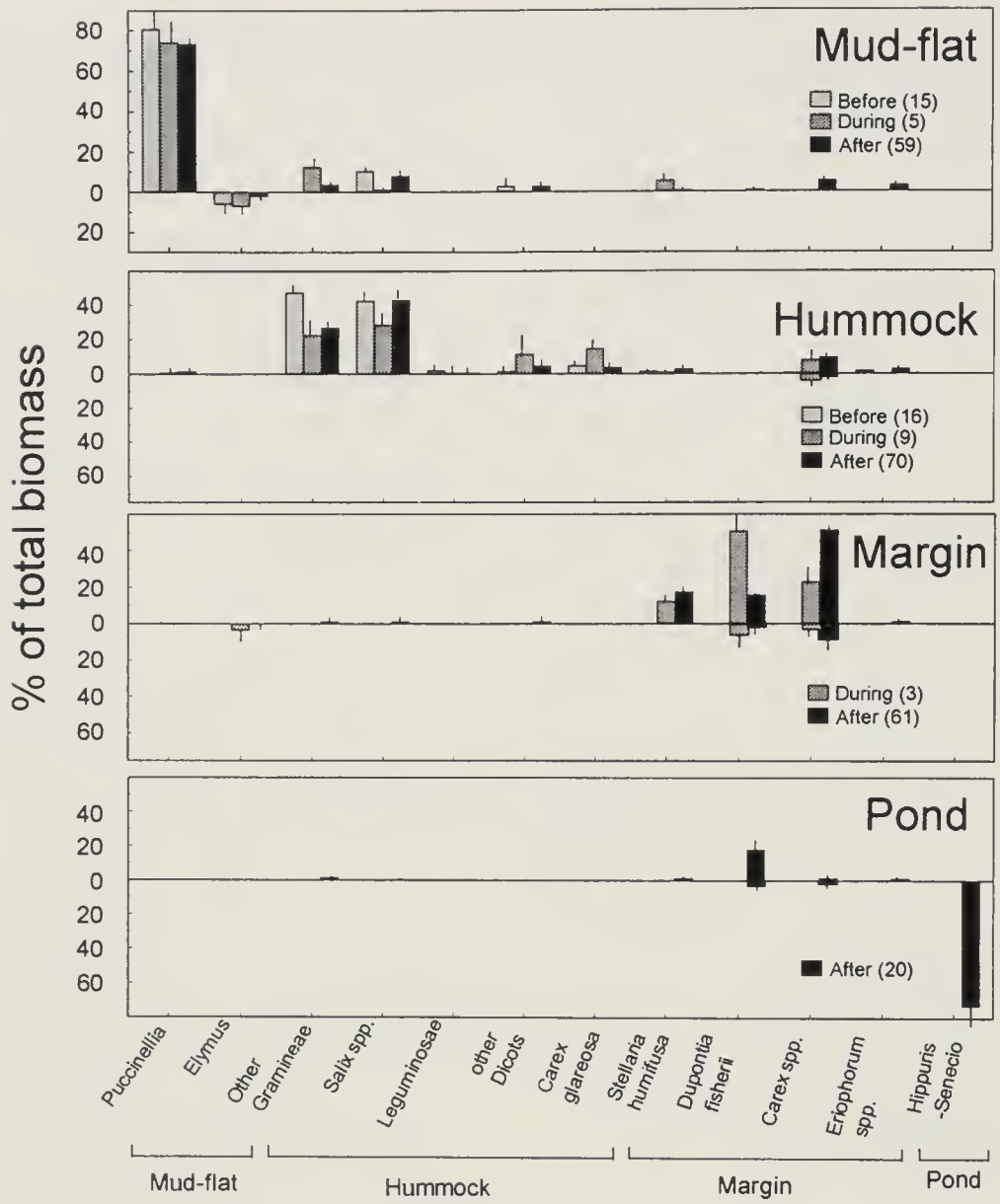

FIG. 2. Relative availability of plants in each snow-free habitat before, during, and after snow melt, measured as the average percent food in dry biomass on the Walker Bay Study Area, NWT, May–June 1993–1994. Sample sizes are given in parentheses, years pooled. Availability of aboveground plant parts is given above the zero line and of below ground plant parts below the zero line.

some rare food plants of the same genus or family that were growing in the same habitat (Table 1, Fig. 2). The validity of the identification of plant fragments in feces was assessed by analyzing plant mixtures of known composition (Holechek and Gross 1982) and by comparing fecal results to esophageal contents of female Canada Geese (Carrière 1996). We could not easily differentiate *Salix arctica* from *Potentilla nivea*, nor discriminate *Dupontia fisheri* and *Eriophorum* spp. from some fragments of other Gramineae and Cyperaccae, respectively. *Potentilla* spp. and *Eriophorum* spp., however, were relatively rare on the study area (Fig. 2, see other Dicots and *Eriophorum* spp.). Some below ground plant parts could not be identified reliably (Carrière 1996). Feces analyses consequently provided only an estimate of use of common above ground food plants on our study area. Coefficients of variation of the proportion of food plants among slides within feces ranged from less than 5% for graminoids to 10–20% for dicots. We defined diet as the average percent of each food plant (% of fragments) present in the feces (frequency of occurrence method; Johnson 1982). Diet was determined for each goose species and snow melt period by pooling years, with individual feces representing sampling units.

We compared use of each food plant among all possible combinations of goose species and snow melt periods using Kruskall-Wallis ANOVA on Ranks tests followed, if significant, by multiple comparison tests (Daniel 1978) using Excel 97.

Feeding techniques.—Use of below ground plant parts was indexed by the proportion of feeding pairs grubbing in each habitat during scans. Conversely, pairs were assumed to eat above ground plant parts while pecking.

We used a Paired *t*-test to determine if the propor-

TABLE 1. Diet of White-fronted and Canada geese before, during, and after snow-melt, from arrival on the nesting grounds to incubation, Walker Bay Study Area, Kent Peninsula, NWT, 1993–94. "Arriving" females were collected before snow-melt, "pre-laying" females during and after snow-melt, and the incubating female after snow-melt.

	Fecal content (% of fragments)														Esophagal content (% dry mass)				
	White-fronted Geese						Canada Geese								Canada Geese (females)				
	Before		During		After		Before		During		After				Arrival		Prelaying		
Food plant	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	H[a]	P	$\bar{x}$	SE	$\bar{x}$	SE	Early inc.
Number of feces or geese	27		13		14		15		43		19				6		9		1
Puccinellia tillers[b]	52	4 C	18	6 AB	5	2 A	73	5 C	24	3 B	9	2 AB	63	<0.001	96	5	27	16	
Elymus arenarius rhizomes	3	1	10	7	tr		tr		1	1	tr		11	0.05					
Other Gramineaes[c]	26	3 BC	29	6 C	17	5 ABC	13	3 A	14	2 AB	29	5 C	20	0.001					
Salix buds[d]	2	0	3	1	2	1	5	1	4	1	5	4	9	>0.05					18
Other dicots[e]	9	2 C	1	1 A	11	5 BC	2	1 AB	4	1 BC	7	3 BC	19	0.002	1	0	5	11	
Stellaria humifusa	tr[i]	A	2	1 AB	2	1 AB	tr	A	12	3 C	5	3 AB	36	<0.001	tr		61	11	
Dupontia Fisheri tillers	tr	A	tr	ABC	11	6 BC			1	1 AB	13	5 C	41	<0.002	3	4			64
Carex spp. tillers[f]	tr	A	23	7 B	20	5 B	tr	A	20	3 B	13	4 B	56	<0.003			1	2	18
Hippuris-Senecio[g]					5	4					3	3							
Carex seeds[f]			tr		1	1			tr		tr						6	7	
Unidentified[h]	7		13		25		6		20		15								

[a] Kruskal-Wallis tests of differences of food use for each goose species-period combination. Results from unplanned multiple comparisons tests are given using capital letters near food use values. Values with different letters differ within each row.

[b] *Puccinellia* spp.: *P. phryganodes, P. arctica.*

[c] Other Gramineae: *Festuca* spp., *Poa* spp., *Calamogrostis* spp., *Arctophila fulva.*

[d] *Salix* spp.: *S. arcticaor S. lanata* closed buds before snow-melt, closed-open buds after snow-melt, open buds-leaves in esophagus.

[e] Other dicots: *Potentilla* spp., *Draba* spp., *Sueda calceoliformis, Astragalus* spp., *Hedysarum* spp., *Oxytropis* spp.

[f] *Carex* spp.: *C. bigelowii, C. salina, C. subspathacea.*

[g] *Hippuris* sp.: *H. vulgaris* or *H. tetraphylla. Senecio* sp.: *S. congestus*, includes rhizomes, young shoots, and leaves.

[h] Unidentified includes fragments of dicots, of *Eriophorum* spp., and all rhizomes except those of *Elymus* sp., and *Hippuris* spp.

[i] tr = trace.

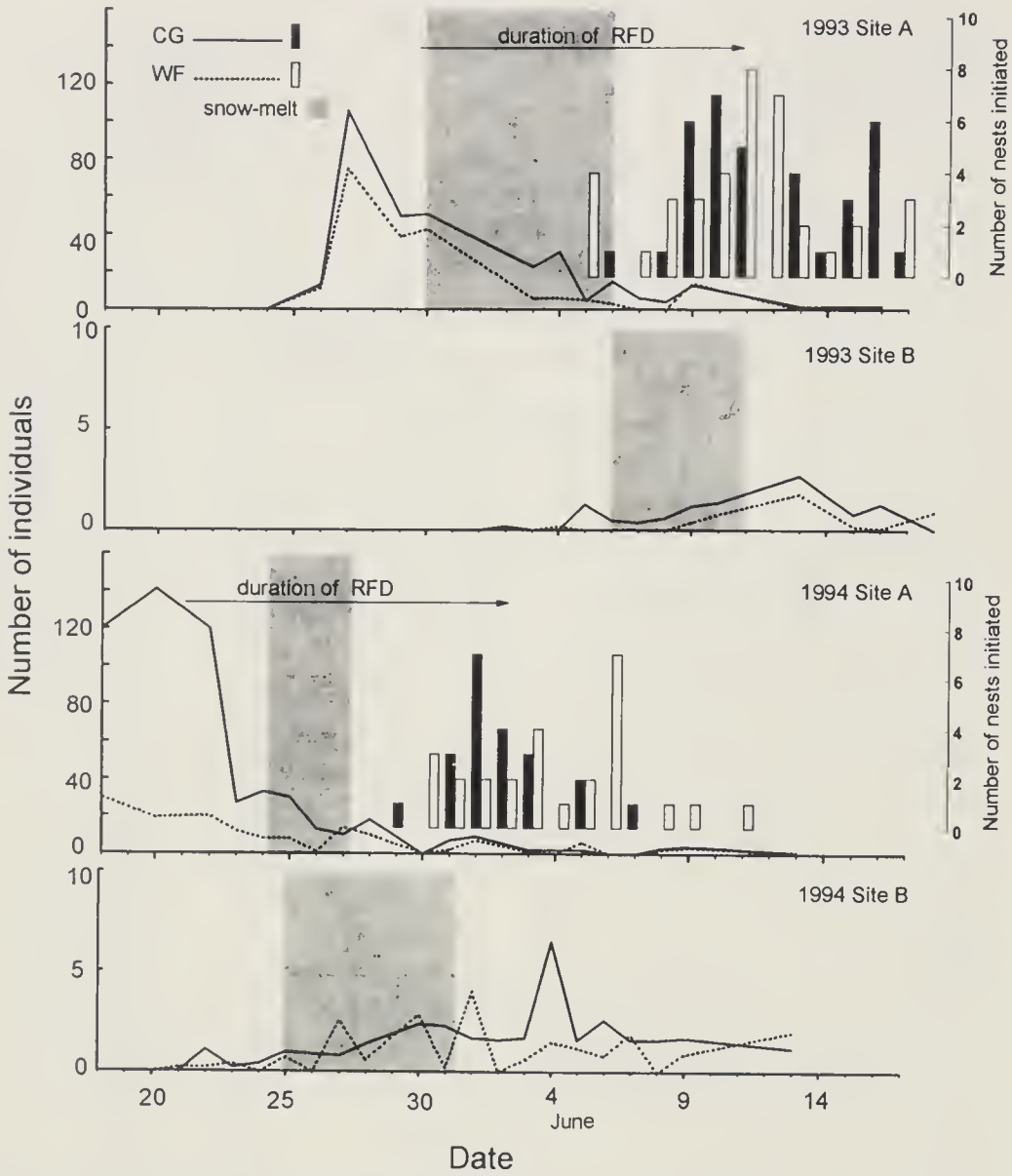

FIG. 3. Number of individual White-fronted Geese (WF) and Canada Geese (CG) counted daily at each station on sites A (n = 2) and B (n = 18; see Fig. 1), from arrival to early incubation, and number of nests initiated daily by each species on the Walker Bay Study Area, NWT, 1993–1994. Arrows indicate duration of rapid follicular development (RFD) for a first egg layed at the median laying date each year. Shaded areas indicate periods of snow melt, defined as 80–20% snow cover. Snow melt pattern on site A was used to define periods for all analyses.

tion of time spent grubbing differed between goose species, pairing observations within habitat-period-year combinations. For each species, we used linear regression to analyze how the proportion (aresine square-root transformed in degrees; Sokal and Rohlf 1981) of time spent grubbing changed with the proportion of below ground biomass available in different habitats, snow melt periods, and years. The short, rapid melting period in 1994 was combined with the after-melt period.

Unless otherwise stated, statistical analyses were performed using SigmaStat™ (version 1.0; Jandel Scientific Software 1993) in the PC DOS and Microsoft® Windows™ operating system. Statistical significance was established at $P \leq 0.05$.

RESULTS

Annual phenology.—Upon our arrival on 20 May 1993 and 17 May 1994, sites A and B were 95% and 99% snow covered, respectively. Hummock and mud-flat habitats located along the river were the only habitats available. Relative to 1987–1996 (R.G.B., unpubl. data), snow melt was early in 1994 and average in 1993 (Fig. 3). In general, snow melted first on dry habitats (mud-flat, hummock), then on wet ones (pond margin, pond), and earlier on site A than on site B (Fig. 3). The periods before snow melt were 10 days (1993)

and 7 days (1994); melting periods were 7 days (1993) and 3 days (1994), and periods after snow melt [end of melting to onset of incubation (median laying date + 4 days)] were 9 days (1993) and 13 days (1994). The total length of the preincubation periods on the nesting ground were thus 26 d in 1993 and 23 d in 1994.

Geese were present along the river (on site A or outside the intensive study area) upon our arrival in 1993 (n = 50–80 pairs) and 1994 (n = 140–150 pairs), but major arrivals occurred around 27 May 1993 and on or prior to 20 May 1994 (see transect surveys: Fig. 3, site A). During snow melt, goose numbers decreased on site A (and from other areas along the river) and increased slightly on site B as geese dispersed from areas along the river to the rest of the study area (Figs. 1, 3).

We are confident that the pairs observed during this study were part of the locally nesting population because about ⅓ of the collared individuals we found nesting in the study area ($n > 11$ of each species per year) were observed on site A and other areas along the river. Individuals collared in other study areas were never observed on Walker Bay Study Area (R.G.B., pers. obs.).

The first nests were found on 5 June 1993 and on 28 May 1994. Median laying dates were 11 June 1993 (White-fronted Goose: n = 38, Canada Goose: n = 35) and 2 June 1994 (White-fronted Goose: n = 26, Canada Goose: n = 21) for both species (Kruskal-Wallis ANOVA on Ranks: $H = 77.4$, $P < 0.001$; medians were different between years only; Fig. 3). The minimum intervals between goose arrival and median laying date were 14 days in 1993 and 13 days in 1994.

Use and selection of habitats.—White-fronted and Canada geese did not differ in their use of habitats before snow melt in either year (G-tests of independence: 1993: G_{adj} = 0.083, 1 df, $P > 0.05$; 1994: G_{adj} = 0.031, 1 df, $P > 0.05$; Fig. 4A, B). Both species also used habitats according to their availability during that period (χ^2 Goodness-of-fit: all $\chi^2 \leq 3.08$, $P > 0.05$).

Habitat use differed between species during snow melt in both years (G-tests of independence: 1993: $G_{adj} = 18.14$, $P < 0.001$; 1994: $G_{adj} = 39.26$, $P < 0.001$). Both species fed in newly available wet habitats (pond margin and pond) during snow-melt, but White-fronted Geese used them more often than did Canada Geese.

Pairwise comparison tests showed that in both years Canada Geese used hummock and mud-flat habitats significantly more often than White-fronted Geese and that White-fronted Geese used wet habitats significantly more often than Canada Geese (Fig. 4C, D).

Similar interspecific differences in habitat use were observed after snow melt in both years (G-test of independence: 1993: G_{adj} = 23.03, $P < 0.001$; 1994 sites pooled: G = 69.44, $P < 0.001$). Pairwise comparison tests showed that White-fronted Geese used ponds (1993 and 1994) and pond margins (1994) significantly more often than Canada Geese (Fig. 4E, F, G).

In 1993, habitat selection (i.e., use vs availability) by both species differed after snow melt (χ^2 Goodness-of-fit: Canada Goose: χ^2 = 94.8, $P < 0.001$; White-fronted Goose: χ^2 = 117.9, $P < 0.001$). Canada Geese preferred (i.e., use > available) mud-flat, pond margin, and pond, and avoided hummock habitats (Fig. 4E). White-fronted Geese preferred pond and avoided hummock habitat (Fig. 4E). In 1994, most geese fed near tower 1 after snow melt (Fig. 1), where the relative availability of habitats differed greatly between site A and B (Fig. 4). Consequently, we analyzed habitat use in each site separately. Data in dry (mud-flat/hummock) and wet (pond margin/pond) habitats were pooled at site B to obtain sufficient sample sizes for χ^2 tests. Near the river (site A), Canada Geese used habitats according to their availability (χ^2 Goodness-of-fit: χ^2 = 0.92, $P > 0.05$; Fig. 4F), while White-fronted Geese preferred pond margin and pond habitats and avoided mud-flat habitats (χ^2 = 49.8, $P < 0.001$). On site B, Canada Geese again used habitats according to their availability (χ^2 = 0.22, $P > 0.05$; Fig. 4G) and White-fronted Geese still preferred wet habitats (pond margin/pond) and avoided dry ones (mud-flat/hummock; χ^2 = 23.4, $P < 0.001$).

Diet.—Nine food types were recognized in feces (Table 1). The number of different food types detected increased as snow melted, as expected because of the increase in available habitats. A major food before snow melt was *Puccinellia* spp. tillers, which accounted for 52% and 73% of White-fronted and Canada

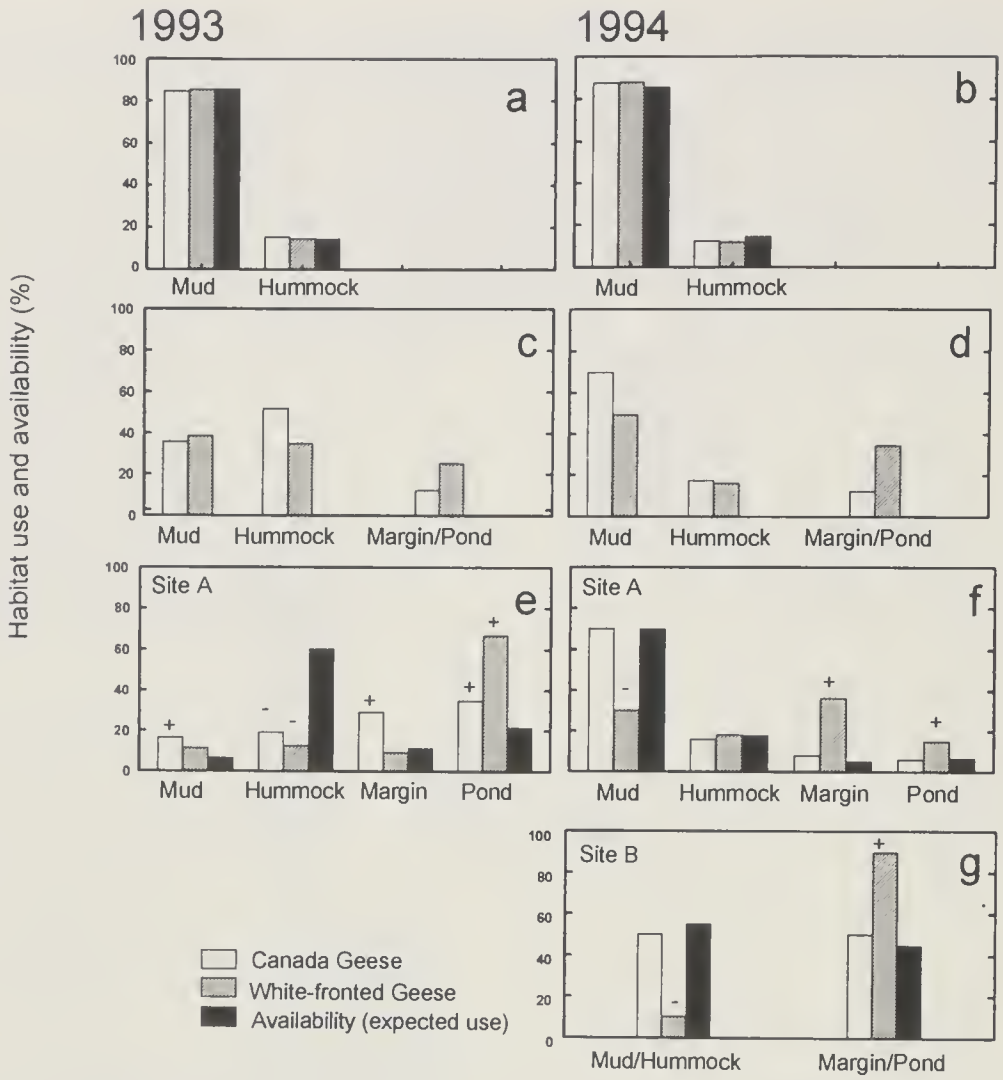

FIG. 4. Use (% of feeding pairs) of mud-flat, hummock, pond margin, and pond habitats by White-fronted (WF) and Canada geese (CG), and availability of these habitats during preincubation on the Walker Bay Study Area, NWT, 1993–1994. (a–b) Before snow melt 1993 (CG: n = 332; WF: n = 228) and 1994 (CG: n = 1265; WF: n = 383). (c–d) During snow melt 1993 (CG: n = 532; WF: n = 137) and 1994 (CG: n = 637; WF: n = 168); habitat availability could not be estimated. (e) After snow melt at site A in 1993 (CG: n = 120; WF: n = 87). (f–g) After snow melt in 1994, site A (CG: n = 50; WF: n = 33) and site B (CG: n = 22; WF: n = 29). A "+" indicates use > availability, "−" indicates use < availability and no symbol indicates use = availability ($P > 0.05$).

goose diet respectively. After snow melt, more than 50% of the diets of White-fronted and Canada geese were composed of *Carex* spp. and *Dupontia fisheri*. For both species, most (85%) feces contained food plants representative of at least 2 habitats. Consequently, changes in diet reflected changes in both habitat use and food use within habitats.

The greater diversity of the diet found in the feces of Canada Geese relative to esophagi (Table 1) is probably caused by the accumulation of food fragments in the digestive system. Nevertheless, analyses of esophageal content indicated that some Gramineae (fragments not identified at the genus level) could be overestimated in fecal analyses, whereas *Stellaria humifusa, Dupontia fisheri,* and *Carex* seeds could be underestimated (see methods, Carrière 1996). Young leaves and open buds of *Salix* spp. were found only in female Canada Geese collected during incubation.

Available biomass.—Plant biomass varied among combinations of habitats and sampling dates for both above ground (Kruskal-Wallis ANOVA on ranks: 1993: H = 46.0, P < 0.001; 1994: H = 152.1, P < 0.001) and below ground plant parts (1993: H = 25.7, P = 0.012; 1994: H = 58.7, P < 0.001; Fig. 5). There was little seasonal increase in total dry biomass within each habitat, except after the median laying date for above ground biomass in pond margins (1994 only) and below

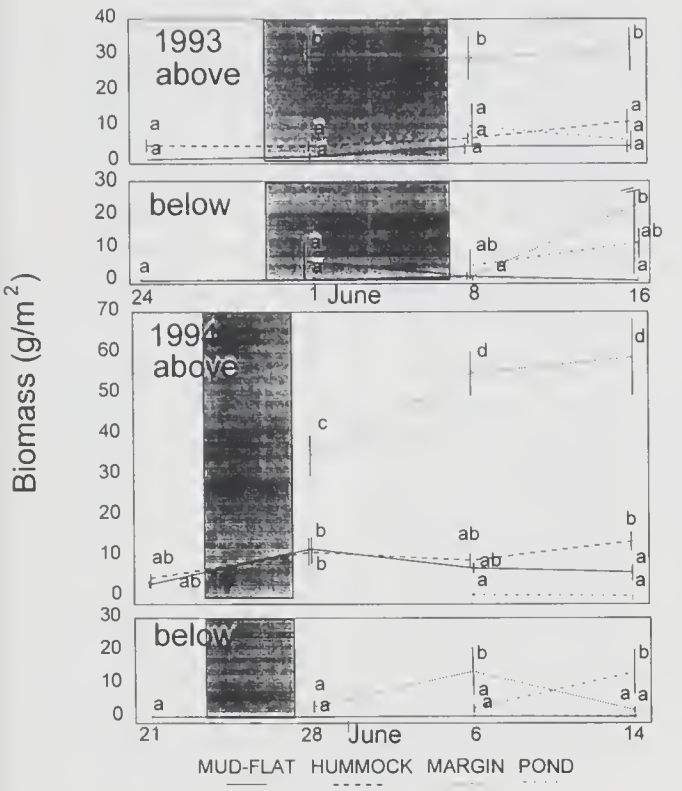

FIG. 5. Live above and below ground dry biomass (mean ± SE) available to geese in 4 habitats during preincubation on the Walker Bay Study Area, NWT, 1993–1994. Values with same letter within graphs do not significantly differ (multiple comparison tests after a Kruskall-Wallis ANOVA on Ranks test for each year, above and below ground biomass tested separately, all tests $P < 0.02$). Grey areas indicate periods of snow melt (80–20% snow cover on site A). Number of sampled 20 × 20 cm quadrats per sampling date were: (1993) mud-flat = 3, 5, 17, 14; hummock = 6, 9, 11, 11; pond margin = NA, 3, 6, 6; pond = NA, NA, 3, 26 and (1994) mud-flat = 12, 16, 24, 23; hummock = 10, 16, 16, 16; pond margin = NA, 17, 16, 16; pond = NA, NA, 16, 20. NA = datum was not available, under snow.

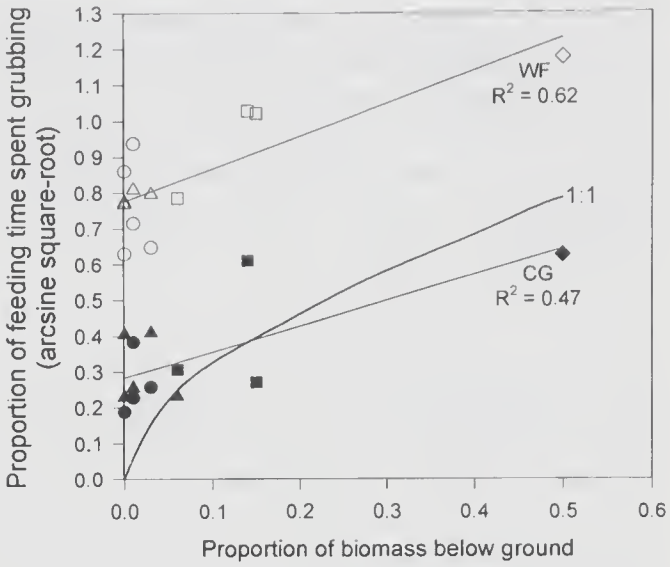

FIG. 6. Relationship between below ground biomass available and proportion of feeding time spent grubbing by female White-fronted (WF) and Canada geese (CG) during preincubation on the Walker Bay Study Area, NWT, 1993–1994. Each point is the proportion of scanned pairs observed grubbing (arcsine square-root transformed) in a habitat during a specific period and year. Closed symbols are Canada Geese, open symbols are White-fronted Geese. Habitats are mud-flat (circles), hummock (squares), pond margin (triangles), and pond (diamonds). Linear regressions: for WF: y = 0.78 + 0.91x [0.50–1.32; ß(95%CI)], F = 18.0, P = 0.001; for CG: y = 0.28 + 0.72x [0.27–1.17; ß(95%CI)], F = 9.9, P = 0.009.

ground biomass in pond margins (1993) and pond (1994). Seasonal changes in below ground biomass were mostly the result of a gradual deepening of the active layer. We pooled sampling dates and found differences in above ground biomass among habitats (Two Way ANOVA: $F = 112.1$, $P < 0.001$) and years ($F = 4.25$, $P = 0.04$; habitat-year interaction, $F = 7.25$, $P < 0.001$). Above ground biomass in pond margins was higher than in any other habitat, particularly in 1994. We found a tendency for below ground biomass to be lower in dry (0–1.08 g/m^2) than in wet habitats (1.33–24.4 g/m^2; Two Way ANOVA: $F = 2.61$, $P = 0.05$), but no difference between years ($F = 1.53$, $P > 0.05$; habitat-year interaction, $F = 4.09$, $P = 0.007$).

Use of below ground food plants.—Canada Goose pairs grubbed less often than White-fronted Geese (Canada Goose: 12.4%, White-fronted Goose: 56.9%; Paired t-test: $t = -14.2$, $P < 0.001$; Fig. 6), which grubbed extensively even in habitats where below-ground biomass was very low (i.e., in mud-flat/hummock), before widespread snow melt and thawing of the ground surface. Spatial distribution of below ground vegetation (mostly *Elymus* sp. rhizomes) was clumped in these habitats and available below ground biomass may have effectively been much higher in some patches used by foraging individuals. In all habitats, before and during snow melt, most of the below ground biomass was frozen under the active layer and hence was not available to geese.

There was a significant positive relationship between the proportion of below ground biomass in different habitat-year-period combinations and the proportion of feeding time

geese spent grubbing in these habitats (linear regression: White-fronted Geese: $F = 18.0$, $P = 0.001$; Canada Geese: $F = 9.9$, $P = 0.009$; Fig. 6). This indicates that both White-fronted and Canada geese modified their feeding behavior with changes in below ground food availability.

DISCUSSION

Arrival, phenology, and timing of laying.—The minimum interval between peak arrival and laying was 1–4 day longer than necessary for rapid follicular development (Alisauskas and Ankney 1992a), which is typical in most goose populations during early and average years (Raveling 1978, Fox and Madsen 1981, Budeau et al. 1991, Gauthier and Tardif 1991, Bromley and Jarvis 1993). Arrival and laying initation were both earlier in 1994 than in 1993 and peak initiation of laying occurred about 15 days after peak arrival in 1993, but apparently only 12–13 days after arrival in 1994. The longer interval in 1993 likely was due to later snow melt that year; nest initiation closely followed snow melt in site B. In contrast, during the early snow melt of 1994, nesting sites became available (i.e., when snow cover <50% in site B) 5–8 days before peak nest initiation, indicating that completion of RFD, rather than snow melt, constrained nesting that year. These relationships were remarkably similar in White-fronted and Canada geese.

The close proximity of prenesting feeding sites to nesting sites conveys benefits to geese arriving on the Arctic nesting grounds before RFD. During both years, pairs of both species dispersed from early exposed locations near the river to additional areas exposed late during snow melt. This resulted in their using feeding areas that were increasingly distant from the river. Such short distance movement by breeding pairs from feeding areas to nearby nesting areas has been observed in other goose populations (Gauthier 1993, Prop and de Vries 1993). This local dispersal is similar to the final migratory flight from staging areas to the breeding grounds in populations where most females nest soon after arrival in the Arctic (Ankney and MacInnes 1978, Wypkema and Ankney 1979). For the latter case, however, the flight occurs late in RFD (Wypkema and Ankney 1979). Unlike geese nesting adjacent to feeding sites, this flight necessarily draws largely upon body reserves during RFD because long migratory flights would use more energy than local dispersal. Furthermore, earlier arrival on the breeding ground enables pairs to directly assess nesting conditions (Wypkema and Ankney 1979, Peterson 1992, Rohwer 1992, Ganter and Cooke 1996).

Although little plant growth occurred, food availability rapidly and greatly increased during preincubation. The change in total available biomass was due to the rapid exposure of habitats with large plant biomasses during snow melt, a common phenomenon in tundra ecosystems (Wielgolaski et al. 1981). This may play an important role in determining individual reproductive decisions in many Arctic nesting geese (Gauthier 1993, Prop and de Vries 1993) because increasing food availability before and during egg-production could improve individual condition (as indexed by body mass; Bromley and Jarvis 1993, Choinière and Gauthier 1995, Ganter and Cooke 1996). Which components of reproductive success (laying date, clutch size, nest attentiveness, condition at hatching, or a combination of these) may be affected by a female's improved body condition depends on the timing of changes in food availability with respect to RFD initiation in individual females (e.g., Bolton et al. 1993, Dalhaug et al. 1996).

Interspecific differences in feeding ecology.—Snow melt, and the concomitant changes in habitat and food availability, enabled us to detect similarities and differences in resource use and selection between White-fronted and Canada geese during preincubation. In both years, both species shared feeding sites and had the same average date of nest initiation (i.e., RFD initiation), hence they could experience the same changes in the availability of resources at similar times relative to their reproductive process.

Both species used habitats opportunistically before snow melt when pair density was highest (up to 600 pairs/km^2 in snow-free areas) and habitat availability lowest (1–20% of study area was snow free). With onset of snow melt, both species dispersed and overall pair density decreased (<40 pairs/km^2).

After snow melt, Canada Geese generally used habitats more opportunistically than White-fronted Geese, which consistently se-

lected wet habitats with high plant biomass. Below ground food plants were used more extensively by White-fronted Geese than by Canada Geese in all habitats. These differences are similar to those reported between *Branta canadensis interior* and *Anser caerulescens caerulescens* on a common staging area on James Bay (Prevett et al. 1985), but unlike our study those differences could be explained in part by segregation of feeding areas.

Although we could not test for density dependent habitat selection because of synchronous changes in habitat availability and in pair density with snow melt, the evidence indicates that interspecific differences in the relative suitability of habitats for feeding exists. Consistent with a release from population density effects in a constant environment (Rosenzweig 1985, Morse 1990), White-fronted Geese changed from opportunistic to selective use of habitats with the highest plant biomass. In contrast, Canada Geese exhibited a relatively weak shift.

We suggest three possible non-exclusive explanations for the interspecific differences in habitat use and diet we observed.

1. Pond margin and pond habitats may be more profitable to White-fronted Geese than to Canada Geese because of the longer and apparently more robust bill morphology of the former (WF culmen is 35.3% and skull is 15.4% longer than CG's; Bolen and Rylander 1978, Gawlik and Slack 1996, R.G.B., unpubl. data). A longer bill may enable White-fronted Geese to be more efficient at grubbing in the ground, presumably giving them easier access to resources buried in a frozen and dry substrate. There is a spectrum of feeding techniques used by geese to obtain food (Bolen and Rylander 1978, Bellrose 1980, Prevett et al. 1985, Ganter and Cooke 1996) but we still know little of how morphology affects the relative efficiency of these techniques among species.

2. White-fronted and Canada geese may differ in their food use because their nutrient requirements for reproduction differ. Protein, fat, and calcium are the most important nutrients required for egg formation (Robbins 1993, Alisauskas and Ankney 1992a). Geese generally switch from a simple, carbohydrate-rich diet before spring migration to a protein-rich one during spring migration and egg production (Mainguy and Thomas 1985, Prevett et al. 1985, Budeau et al. 1991, Alisauskas and Ankney 1992b, Bromley and Jarvis 1993, Gauthier 1993), suggesting that protein is a limiting nutrient to egg formation in geese (Krapu and Reinecke 1992). Incubating females mainly require large fat reserves for maintenance (Raveling 1979, Le Maho et al. 1981, Boismenu et al. 1992). Nutrient requirements for egg formation and incubation therefore differ, and whether a female should select for protein or energy rich food during egg production will depend on her initial nutrient reserves, and on how requirements are met through food intake and reserve reallocation.

How females allot nutrients ingested during preincubation to short (egg production) and long term (incubation) requirements may be reflected in their incubation behavior (Bromley 1984, Thompson and Raveling 1987). White-fronted Geese have cryptic nesting behavior, and like Emperor and Giant Canada (*B. c. maxima*) geese, rely mostly on stored nutrients for incubation (mean feeding time per day = 1–8 min; Thompson and Raveling 1987; R.G.B., unpubl. data). In the central Canadian Arctic, Canada Geese nest openly, defend their nests, and take frequent recesses to feed (mean: 40 min per day; Jarvis and Bromley, in press; R.G.B., unpubl. data). Little feeding during incubation by White-fronted Geese suggests a greater requirement for energy rich food prior to incubation. Longer incubation recesses by Canada Geese imply a greater reliance on foraging to meet nutrient requirements during incubation, allowing for more nutrients (e.g., protein) ingested prior to incubation for egg production (see Thompson and Raveling 1987). Thompson and Raveling (1987) suggested that greater incubation attentiveness may be related to larger body size in geese, because they are vulnerable to different types of predators and have a greater fasting endurance (Calder 1974, Boismenu et al. 1992).

3. For Canada Geese, feeding pair density may not entirely reflect the suitability of the habitat for feeding during laying (Van Horne 1983). Canada Geese typically nest on pond margins (R.G.B., unpubl. data), and as laying time approaches pairs may show increasing territorial behavior in some patches of this habitat. Intraspecific aggressive behavior was

observed, and could exclude conspecifics from some patches of pond margins. In contrast, White-fronted Geese prefer hummock habitat to nest in, and their territorial behavior appears much weaker (R.G.B. and S.C., pers. obs.).

Potential for competition.—Interspecific competition for habitat and food in spring is believed to be minimal in geese because species usually segregate either spatially (different ranges: Bellrose 1980, Ebbinge et al. 1982, Owen and Black 1990; different feeding habitats: Fox et al. 1992) or temporally (different timing of breeding: Fox et al. 1992). We documented differences in the feeding ecology of two sympatric goose species that nest in synchrony and differ mostly in bill morphology, slightly in body mass, and in incubation behavior. We did not examine niche shifts with changes in the relative densities of each species during spring (Madsen and Mortensen 1987) because both species experienced similar decreases in pair densities with snow melt. Nonetheless, we showed that both species overlapped in habitat use but each differed in its preferred feeding technique and hence in its selection of plant parts ("niche complementarity"; see Nudds 1992). On our study area, potential for both intra- and interspecific competition for food is highest before snow melt, when food availability and diversity are low, and pair density is high.

Interactions between nutrient requirements, foraging ability and food profitabilities (hence habitat selection: Stephens and Krebs 1986) in goose species with similar body sizes but with different bill morphologies warrant further study.

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A TEST OF THE CONDITION-BIAS HYPOTHESIS YIELDS DIFFERENT RESULTS FOR TWO SPECIES OF SPARROWHAWKS (*ACCIPITER*)

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ABSTRACT.—The determination of body condition of birds is important for many field studies. However, when using trapping methods based on food as a lure, the sample of trapped birds could be biased toward individuals in poor physical condition. We provide information on body mass, body condition, and sex and age ratio of Levant Sparrowhawks (*Accipiter brevipes*) and Eurasian Sparrowhawks (*Accipiter nisus*) caught in Elat, southern Israel, during spring migration. We compared physical condition of birds trapped in baited traps to physical condition of birds trapped in mist nets (no bait). The body mass and index of physical condition of migrating Levant Sparrowhawks trapped in baited traps was lower than birds trapped in mist nets. By comparison no differences were detected in body mass and condition index of migrating Eurasian Sparrowhawks caught by the different trapping methods. The differences found in condition of Levant Sparrowhawks trapped with and without food support the predictions of the condition-bias hypothesis; however, data from the Eurasian Sparrowhawk do not. The extent to which biases occur may be different even for closely related species. *Received 1 Oct. 1998, accepted 7 Jan. 1999.*

Using food to trap animals, especially predators, is probably the most widespread capture method used by biologists. The capture of birds of prey involves many methods, most of which use small birds and rodents as lures (Clark 1981, Bloom 1987). These trapping methods are vulnerable to sampling bias because hungry birds in poor condition are more likely to overcome their fear of entering traps compared to birds in good condition (Weatherhead and Greenwood 1981). Considerable support for this condition-bias hypothesis comes from studies of songbirds (Weatherhead and Greenwood 1981, Dufour and Weatherhead 1991) and ducks (Greenwood et al. 1986, Hepp et al. 1986, Reinecke and Shaiffer 1988, Conroy et al. 1989). We know of no such studies conducted on birds of prey.

Two species of sparrowhawks occur regularly during spring migration at Elat, Israel. The Levant Sparrowhawk (*Accipiter brevipes*) breeds in Russia, eastern Europe, and the Balkans. It migrates in large flocks to Africa in September, returning in May (Cramp and Simmons 1980). In autumn sparrowhawks pass over northern Israel between mid-September and the beginning of October; up to 41,700 birds were counted during one autumn (Leshem and Yom-Tov 1996). During spring they return through southern Israel between 20 April and the beginning of May, with up to 49,800 birds counted during one season (Clark et al. 1986, Shirihai 1996). The Eurasian Sparrowhawk (*Accipiter nisus*) breeds across the Palearctic region (Newton 1986). In contrast to the Levant Sparrowhawk only a few hundred Eurasian Sparrowhawks pass through Israel during autumn (Dovrat 1986, Leshem and Yom-Tov 1996) and spring (Clark et al. 1986, Shirihai 1996).

Physical condition during spring migration is significant, not only for the successful completion of the migratory journey, but also for the timing of arrival at the breeding grounds and the condition of nutrient reserves required for successful breeding. The breeding success of birds in the temperate zone typically declines as the breeding season progresses. Body condition and amount of nutrient reserves have been shown to affect breeding success in a variety of species (Korschgen 1977, Moss and Watson 1984, Newton 1986). McLandress and Raveling (1981) demonstrated the importance of spring nutrient reserves for migration as well as for reproduction and their effect on clutch size in Canada Geese (*Branta canadensis*). Price and coworkers (1988) suggested that the ability to accumulate sufficient reserves required for breeding may prevent the evolution of progressively earlier breeding dates. Spring migrants arrive in Elat after crossing desert areas where feed-

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ing opportunities are probably limited. Thus, it is important to investigate the occurrence of condition biases which may go undetected and lead to misinterpretation of data collected from trapped birds (Weatherhead and Greenwood 1981, Gorney and Yom-Tov 1994).

In conjunction with a spring migration raptor banding project, we captured Eurasian and Levant sparrowhawks using a variety of trapping methods. Our objective was to test the condition-bias hypothesis in birds of prey and to compare the physical condition of spring migrants to condition of pre-breeding sparrowhawks.

METHODS

Migrating sparrowhawks were captured as part of a raptor banding project during five consecutive spring migration seasons between March and May in 1984–1988, in the agricultural areas just north of Elat (29° 33′ N 34° 55′ E), Israel (Clark et al. 1986). Birds were caught in mist nets, bal-chatri traps, and bow nets (Bloom 1987) commonly used by hawk researchers in North America and conforming to regulations applied there. Only bal-chatri and bow-nets were placed on the ground using food as a lure. Three-meter tall, 4 shelf mist nets were placed in palm groves along rows of trees used for roosting by sparrowhawks. The distance between the lured traps and mist nets was generally at least 500 m. Occasionally small birds were caught in mist nets and they may have lured some sparrowhawks into the nets. Such cases were excluded from the data analysis when detected.

All birds were measured, weighed to the nearest 1 g, and banded before release. Wing chord (straight line from wrist to wing tip, without stretching or flattening the wing) was measured with a ruler to the nearest 1 mm. Culmen length was measured to 0.1 mm using Manostat calipers. Age and sex were determined by plumage, eye color, and size (Cramp and Simmons 1980). Age was determined as either adult (two years old or more) or yearling (approximately one year old, i.e., birds in their second calendar year).

We compared the body mass and body condition index (body mass/wing chord × culmen length) of Levant and Eurasian sparrowhawks that were caught in mist nets to those that were caught in baited traps (bal-chatri and bow-nets). Comparisons were conducted on four groups: adult and yearling females, and adult and yearling males. Sample sizes vary slightly because we lack measurements for several individuals. This particular physical condition index was used because of its high correlation with fat reserves in migrating Steppe Buzzards (*Buteo buteo vulpinus;* Gorney and Yom-Tov 1994). We found similar results however, using the more commonly employed index of body mass divided by wing length.

To test whether birds in poorer body condition are more likely to be attracted to baited traps than birds in better condition, we compared for each age and sex category the body mass and condition index of birds trapped with baited traps and birds trapped in mist nets (no bait). We also compared the number of individuals from each age and sex class that were trapped in baited and non-baited traps.

We used Abstat and Minitab 6.1.1 programs for IBM compatable computer for statistical analysis. All variables were tested for normality. When assumptions were met we used separate SD *t*-tests. If normality assumptions were not met we used Mann-Whitney tests. All probabilities are two-tailed.

RESULTS

Levant Sparrowhawk.—Although Levant Sparrowhawks pass through Elat during three weeks, we captured 90% of all age and sex categories within a mean of 9.4 (yearling males) and 10.5 (adult females) days (means calculated for 5 years of the study). Although the passage for this species is concentrated and rapid, adults were trapped earlier than yearlings with median capture dates of 24 April for adult males, 25 April for adult females and 26 April for yearling males and females. We caught 425 Levant Sparrowhawks, 404 of which we sexed and aged. Slightly more yearlings were trapped (52%) than adults (48%) at Elat. Sex ratio deviated from the expected 1:1 ratio in favor of males in both adults (61.1% males, 38.9% females; $n = 193$; $\chi^2 = 9.58$, $P = 0.002$), and yearlings (56.9% males, 43.1% females; $n = 211$; $\chi^2 = 3.98$, $P = 0.046$).

Body masses of adult males and females were significantly larger than those of yearlings (Table 1). We found no significant differences between condition indices of adult and yearling birds (Table 1). Thus, much of the difference in mass appeared to be due to the smaller size of yearling birds (Table 1). We also found no significant associations within age and sex groups between date of migration and physical condition, nor did the physical condition of trapped birds vary with time of day.

Mean condition index of adult females was significantly higher than condition index of adult males (Mann-Whitney $U = 1862$, $P = 0.001$, two-tailed test). Similarly yearling females were in better condition than yearling males (Mann-Whitney $U = 1740$, $P = 0.001$, two-tailed test).

We found no significant differences be-

TABLE 1. Body mass (g), wing chord (mm), and condition index (body mass/wing chord × culmen length) of adult and yearling male and female Levant Sparrowhawks caught in Elat 1984–1988.

Group	Body mass (g)					Wing chord (mm)					Condition index				
	Mean	SD	*n*	*t*	*P*	Mean	SD	*n*	*t*	*P*	Mean	SD	*n*	*t*	*P*
Adult male	169	17	18			217	6	118			0.062	0.007	94		
Yearling male	159	16	120	4.4	<0.001	209	5	120	10.9	<0.001	0.061	0.006	83	1.1	<0.05
Adult female	215	25	69			234	5	70			0.065	0.007	58		
Yearling female	199	20	88	4.0	<0.001	224	5	90	10.4	<0.001	0.065	0.006	65	0.5	<0.05

tween males and females ($\chi^2 = 0.313$, $P > 0.05$, df = 1) nor between adults and yearlings ($\chi^2 = 0.024$, $P > 0.05$, df = 1) in proportion of birds trapped in baited and non-baited traps. The mean body mass and mean condition index of adult males and yearling females trapped in mist nets was higher than the mean body mass and condition index of birds trapped in baited traps ($P < 0.05$; Table 2). Adult females and yearling males demonstrated no difference in mean condition index between both kinds of traps (Table 2).

Eurasian Sparrowhawks.—Most Eurasian Sparrowhawks (90%) pass through Elat in five weeks. As with Levant Sparrowhawks, adults were trapped before yearlings. Median capture date was 14 April for adult males and females, 20 April for yearling females and 22 April for yearling males. We trapped 72 Eurasian Sparrowhawks, with slightly more yearlings (53%) than adults (47%). Sex ratio among adults ($n = 35$; 43% males, 75% females), did not deviate from the expected 1:1 ratio ($\chi^2 = 1.48$, $P > 0.05$), but did deviate among young birds in favor of females ($n = 37$; 27% males, 73% females; $\chi^2 = 7.81$, $P = 0.005$).

Mean body mass of adult females was significantly larger than that of yearling females ($P < 0.05$), and their wing chord was significantly longer ($P < 0.01$; Table 3). However, the large body mass of adult females was not due to size difference alone since their physical condition index was significantly higher than that of yearling females ($P < 0.05$; Table 3). We also found no significant difference in mean body mass or physical condition index between adult and yearling males (Table 3). However, the wing chord of adult males was significantly longer than that of yearling males ($P < 0.01$; Table 3). Females in both age groups had significantly higher condition indices than males (Mann-Whitney $U = 13$, $P < 0.001$; $U = 65$, $P = 0.04$, for adults and yearlings, respectively). No association was found between index of physical condition and between time of day and date of capture.

We found no significant differences in body mass and condition indices between Eurasian Sparrowhawks trapped in lured traps and in mist nets. Significantly more females (33 of 48) than males (6 of 18) were trapped in baited traps ($\chi^2 = 12.3$, $P < 0.001$, df = 1). A similar proportion of adults (16 of 35) and

TABLE 2. Comparison of body mass and condition index of Levant Sparrowhawks caught in mist nets (no lures) and in lured traps, Elat 1984–1988.

	Mistnets			Lured traps			Comparison	
	n	Mean	SD	*n*	Mean	SD	*t*	*P*
Body mass								
Adult females	19	213	27	39	219	23	0.74	>0.05
Adult males	35	175	18	61	167	17	2.06	0.043
Yearling females	22	208	16	49	197	21	2.42	0.019
Yearling males	29	162	19	55	157	14	1.14	<0.05
							Mann-Whitney	
							W	*P*
Condition index								
Adult females	19	0.065	0.007	39	0.065	0.007	1142	>0.05
Adult males	34	0.064	0.008	60	0.061	0.006	2568	0.027
Yearling females	21	0.068	0.005	44	0.063	0.006	1261	0.008
Yearling males	29	0.062	0.007	54	0.060	0.006	2124	>0.05

yearlings (23 of 37) were trapped in baited traps ($\chi^2 = 1.96$; $P > 0.05$, df = 1).

DISCUSSION

Physical condition of migrants trapped with food as a lure may be subject to biases (Weatherhead and Greenwood 1981). One of the prominent differences we found between the two *Accipiter* species is that the condition index of Levant Sparrowhawks captured with and without food as a lure supports the condition-bias hypothesis, but we found no evidence for a condition-bias for Eurasian Sparrowhawks. Thus, the occurrence and extent of a condition-bias may be different even for closely related species of approximately the same body size trapped during the same study using the same traps. Although few data are available to determine the cause of this difference, several aspects of their migration strategies may be pertinent. Physical condition of birds on the wintering grounds, and food availability could differ for the two species. In addition, they may differ in their tendencies to hunt during migration. Levant Sparrowhawks migrate mainly in large flocks whereas Eurasian Sparrowhawks migrate singly (Cramp and Simmons 1980, Shirihai 1996). Levant Sparrowhawks might not regularly hunt in areas like Elat where many birds would be unlikely to find food. Therefore only weak individuals would hunt and the species would demonstrate a condition-bias. On the other hand, all Eurasian Sparrowhawks may hunt regularly as has been described from other migrating populations and species (Rudebeck 1950, Cochran 1972, Newton 1986) and thus show no evidence for a condition-bias.

When baited traps are used, age bias can occur with more younger birds trapped than older individuals (Nass 1964). Indeed, more yearling than adult Steppe Buzzards were trapped in Elat during the same years (Gorney and Yom-Tov 1994). However, we detected no age bias in the capturing of the two *Accipiter* species.

Migrating Eurasian Sparrowhawks do not appear to store extra fat for migration. Moritz and Vauk (1976) found that birds trapped during autumn and spring migration at Helgoland weighed the same as non-migrating individuals caught at the same time. Extra fattening is probably unnecessary because sparrowhawks in some regions migrate with their prey species, and thus can obtain food along the way (Rudebeck 1950, Cochran 1972, Newton 1986). The spring migrants in our study weighed considerably less than birds at other times of year. The mean body masses of adult Eurasian Sparrowhawks in our study were 33 g (females) and 14 g (males), lower than the mean for European birds (Cramp and Simmons 1980) and 20 g lower for both males and females than birds from the former Soviet Union (Dementiev 1966). The mass difference between migrants and non-migrants is not the result of size differences between populations.

TABLE 3. Body mass (g), wing chord (mm), and condition index (body mass/wing chord × culmen length) of adult and yearling male and female Eurasian Sparrowhawks caught in Elat 1984–1988.

Group	Body mass (g)					Wing chord (mm)				Condition index			
	Mean	SD	*n*	*W*	*P*	Mean	SD	*n*	*W*	*P*	Mean	SD	*n*	*W*	*P*
Adult male	130	10	15			204	6	15			0.055	0.006	15		
Yearling male	139	39	10	174.5	<0.05	196	6	10	219	0.011	0.062	0.016	10	177	>0.05
Adult female	231	22	20			237	6	21			0.070	0.007	20		
Yearling female	214	20	27	589.5	0.019	232	4	25	612	0.009	0.065	0.006	24	541	0.033

Mean wing length of adult Eurasian Sparrowhawks in our study was the same as reported by Cramp and Simmons (1980) and Dementiev (1966). The lower body mass of birds during migration likely reflects reserves used for migration over deserts where chances for feeding are probably minimal. A similar comparison of body mass of Levant Sparrowhawks during migration and at other times of year was not possible because body mass data are not available for non-migration periods. Levant Sparrowhawk's wing chord data from our study are similar to data of Cramp and Simmons (1980) and Dementiev (1966), also to data from a 1996 study conducted in Elat (Clark and Yosef 1997).

Our finding that Eurasian Sparrowhawks migrating during spring weigh less than birds at other times of year is not unique to this species. The mean mass of spring migrating Steppe Buzzards in Elat was significantly lower than for the same species on their wintering grounds in southern Africa (Gorney and Yom-Tov 1994). Adult Eleonora's Falcons (*Falco elenorae*) during migration weighed 100 g less than adults on their breeding grounds (Cramp and Simmons 1980). Although data were not available for Levant Sparrowhawks, it is likely that they also lose weight during migration. In general birds are more likely to demonstrate considerable mass declines during spring migration in Elat because they must cover large stretches of desert on their way from Africa. Upon entering the Mediterranean area north of Elat these species probably begin replenishing their reserves (Yom-Tov and Ben-Shahar 1995). Indeed, Levant Sparrowhawks in autumn were not attracted to the same food in bal-chatri traps that attracted them during spring migration (E.G., pers. obs.).

Adults migrate in spring before young birds in most raptor species probably because of benefits they receive from early arrival to the breeding territories (Newton 1979, Kerlinger 1989). Their earlier passage is undoubtedly aided by better physical condition. In support of this, several researchers found larger fat reserves in adults than in immature birds (Dunn et al. 1988, Serie and Sharp 1989, Alerstam and Lindstrom 1990, Morton et al. 1990, Gorney and Yom-Tov 1994; but see Alerstam and Lindstrom 1990). Our data from this study of

two *Accipiter* species also demonstrate earlier trapping dates of adult than yearling birds. However, we found no difference in physical condition of Levant Sparrowhawks between adults and yearlings. In addition, Eurasian Sparrowhawk adult females were in significantly better condition than yearling females; however, we found no such trend among males.

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THE DEVELOPMENT OF A VOCAL THERMOREGULATORY RESPONSE TO TEMPERATURE IN EMBRYOS OF THE DOMESTIC CHICKEN

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ABSTRACT.—We examined the vocal responsiveness of chicken (*Gallus gallus*) embryos at the pipped egg stage to determine if they were able to regulate their thermal environment by soliciting heat from a surrogate parent. There was no overall effect on vocalizations of exposure to 20° C or 45° C relative to the normal incubation temperature of 37.8° C. There was, however, a general trend towards increased calling as the time of hatching approached. There was also some indication that embryos tested in the late stages of hatching (ringing) vocalized more in the cold, then became relatively silent when rewarmed. When cold-challenged embryos were given 2 min of rewarming (surrogate brooding) in response to their calls body temperature was slightly but significantly elevated above cold only exposed controls. Unlike previously reported anecdotal evidence suggesting a strong vocal response to cold, our results suggest chicken embryos show only weak incipient vocal response to temperature that begins to increase late in incubation and becomes fully functional only after hatching. Unlike other species tested to date, the developmental progression of behavioral and metabolic thermoregulation appear to be tightly linked in this species. *Received 27 Feb. 1998, accepted 5 Oct. 1998.*

The embryos of many avian species are capable of vocalizations prior to hatch (Freeman and Vince 1974; reviewed in Evans 1988a). Embryonic vocalizations may facilitate the transition from incubating eggs to brooding and feeding young (Impekoven 1973; Templeton 1983; Evans 1988a, b), may function as antecedents to post-hatching social behavior (Tuculescu and Griswold 1983), or may function in soliciting care from parents. The embryos of several species respond to cold by increasing vocalizations (Evans 1990a; Bugden and Evans 1991; Evans et al. 1994, 1995; Brua et al. 1996). These vocalizations affect parental behavior and may elicit more attentive incubation (Evans 1989, 1990b, 1992; Brua 1996).

When cold-induced vocalizations trigger rewarming by a surrogate parent in altricial pelicans and semiprecocial gulls, cold-challenged embryos can vocally regulate their body temperatures at relatively safe levels (Evans 1990a; Evans et al. 1994, 1995). In these species such vocal behavioral thermoregulation evidently precedes their ability to thermoregulate endothermically; altricial and semiprecocial species show no apparent metabolic response to cooling before hatching (Matsunaga et al. 1989, Kuroda et al. 1990). However, in precocial species there is evidence that gradual cooling of late stage embryos brings about a small but measurable incipient endothermic response (Freeman 1964, Tazawa et al. 1988, Kuroda et al. 1990). The relationship between the emergence of endothermy and the timing of a vocal response to cold in precocial species is unknown. We examined this issue in the precocial domestic chicken (*Gallus gallus*).

Chicken embryos are capable of vocalizations 2–3 days prior to hatch, but these vocalizations become more frequent during the final 24 hours before hatching (Gottlieb and Vandenbergh 1968, Dawes 1981, Tuculescu and Griswold 1983). In response to the loud calls ("distress calls", Collias 1987) of embryos, hens will vocalize or move around on the nest (Tuculescu and Griswold 1983). Following the maternal response the embryos become silent or emit soft trill calls ("pleasure calls", Collias 1987).

Study of the vocal response of chicken embryos to cold has produced variable results. Early investigation suggested that a pipped egg that was alternately cooled and warmed would give "distress" calls or "pleasure" calls in close correspondence to the temperature changes (Collias 1952). Subsequent studies have shown decreased vocal activity (Oppenheim and Levin 1974), increased vocal activity (Evans 1988a), and inconsistent vocal

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responses (Dawes 1981). Some evidence also suggests that chicken embryos increase their rate of vocalization during exposure to high temperatures (Oppenheim and Levin 1974).

This study was designed to systematically reassess the vocal response of late stage chicken embryos to temperature. We examined the effects of temperatures both above and below the normal incubation temperature, and the effectiveness of call-induced rewarming bouts in the regulation of temperature during cold challenge.

METHODS

White Leghorn Chicken eggs were incubated in a forced air commercial poultry incubator (Perersime Model no. 1) that maintained conditions within a suitable range (37.8 ± 0.5° C and 65 ± 5% relative humidity). Only externally pipped eggs, which are known to be capable of vocalizations (Tuculescu and Griswold 1983), were selected for study.

Effects of continuous chilling and heating.—To examine the vocal response of embryos to low or high temperature, pipped eggs were placed singly, pip hole up, within an environmental chamber that consisted of a coil of copper tubing surrounded by insulating Styrofoam. The temperature in the chamber was controlled by pumping water from controlled water baths (±0.5° C) through the coil surrounding the egg. Testing began with a 10 min pre-test at the control temperature (37.8° C). The coil temperature was then changed to the experimental (20° C or 45° C) or left at the control temperature (37.8° C) for 30 minutes. This was followed by a 10 min post-test period at 37.8° C.

The body temperature of the embryo was measured with a thermocouple placed approximately 1 cm directly into the pip hole. The thermocouple was surrounded by deep lying portions of the embryo's body, away from the outer shell. It was held in place by porous adhesive tape ("Microporc") applied to the exterior of the shell. The body temperature of the embryo and the coil temperature were recorded to the nearest 0.1° C every 30 s by a data logger [Grant Instrument (Cambridge) Model 1203]. Calls with a minimum intensity of 78 dB (2.5 cm from the pip hole, B-fast scale) were recorded by a microphone set in the plexiglass lid of the chamber, connected to a sound operated relay and an Esterline Angus event recorder.

Vocal regulation of temperature during cold challenge.—The apparatus was similar to that described above except that calling of the embryo triggered a period of rewarming (illustrated in Evans 1990a). The embryo faced a continuous cold challenge at 20° C until 5 calls were given. The fifth call then triggered a 2 min period of rewarming with water at 37.8° C being pumped through the coil surrounding the egg. This period of rewarming was followed by a return to default chilling at 20° C until another bout of calling was initiated. If an embryo called in response to each successive period of cold challenge it would in effect be capable of regulating ambient, and hence body temperature (Evans 1990a, Bugden and Evans 1997). Control embryos were placed in the same apparatus and held at a constant 37.8° C throughout. Calls in the control situation triggered a mock warming bout where the same timer and pumps were activated as in the cold challenge situation but the water circulating through the coil remained at 37.8° C. All temperatures were recorded as in the first experiment. An Esterline event recorder recorded both individual calls and the warming and mock warming bouts. Control and cold challenge tests lasted for 1 hour on separate samples of eggs.

To determine when during the pip-to-hatch interval the vocal response to cold might develop, the timing of pipping, hatching, and testing were recorded at 4 h intervals. Short term exposure of pipped eggs to moderate cold can delay hatching in domestic chickens (Evans 1990c). Testing of the eggs at 20° C in this experiment thus could potentially affect the timing of their hatching and so distort the interpretation of the developmental onset of the vocal response to cold. To control for this possibility, the pip-to-hatch intervals of cold challenged and control embryos were compared with a separate sample of embryos (untested control embyros) that were not tested and left to hatch normally in the incubator. Statistical tests were done with STATISTIX (version 4.1, Analytical Software, IBM platform).

RESULTS

Effects of continuous chilling and heating.—Seven chicken embryos exposed to a 30 minute period of chilling at 20° C experienced a fall in body temperature of 8.0 ± 0.3° C (mean ± SE) from 36.9 ± 0.2° C at the start to 28.8 ± 0.3° C at the end of the exposure period. These embryos had a mean calling rate of 10.2 ± 6.8 calls per minute. This result was skewed by two highly vocal embryos that were nearly hatched (ringing stage, Freeman and Vince 1973) by the end of the test. The remaining five embryos were completely silent during their exposure to cold, resulting in a median call rate of 0.0 calls per minute. The body temperature of embryos held at the control temperature of 37.8° C shifted by 0.5 ± 0.1° C, from 37.0 ± 0.2° C to 37.5 ± 0.2° C. None of the 7 control embryos reached the ringing stage and all were relatively quiet during the test period with a mean calling rate of 0.1 ± 0.04 (median of 0.1) calls per minute.

Body temperature of seven embryos exposed to 45° C rose by an average of 4.1 ± 0.3° C, from 36.3 ± 0.2° C to 40.4 ± 0.4° C. Call rate averaged 1.2 ± 0.7 calls per minute

with a median of 0.5 calls per minute. While 2 of these embryos were in the ringed stage, their call rates (1.7 and 0.5 calls/min) were similar to the overall average call rate for this group. A Kruskal-Wallis one way nonparametric ANOVA showed no overall differences in calling rates of chicken embryos at the three temperatures ($H = 4.14$, $P > 0.05$, df = 2).

Vocal regulation of temperature during cold challenge.—Thirty-three embryos were tested under cold challenge experimental conditions (20° C) and 34 were tested as warm-only (37.8° C) controls. There was no significant difference in the time from pipping to the time of hatching in cold challenged, control, and 12 untested control embryos (One way ANOVA: $F_{2,76} = 1.34$, $P > 0.05$). For additional analyses embryos were grouped according to time between testing and hatching. There were 8, 13, and 12 embryos tested under cold challenge and 13, 12, and 9 embryos tested as warm only controls for three developmental categories 0–2.5, 2.5–7.5 and >7.5 h before hatching. The vocal response of cold challenged embryos was greater than that of the warm only controls in all developmental categories (Fig. 1). However, *a priori* two-sample *t*-tests between cold experimental and warm controls showed no significant difference in any of the developmental categories (0–2.5: $t = 0.93$, $P > 0.05$; 2.5–7.5: $t = 0.44$, $P > 0.05$; >7.5: $t = 1.63$, $P > 0.05$).

Within 2.5 h of hatching, the mean number of warming or mock warming bouts increased in both the cold challenged embryos and in the warm only controls (Fig. 1). Since cold exposure produced no significant difference in vocal response, all data were combined for further comparison of vocal response with respect to time before hatch. Embryos vocalized significantly more frequently as the time of hatching approached (Kruskal-Wallis ANOVA: $H = 11.10$, $P < 0.01$, df = 2).

The pattern of calling during the 2 min rewarming and mock rewarming bouts provided an additional measurement of the response to temperature (Table 1). Because of a 6 s delay of the chamber to temperature changes, cold challenged embryos were still experiencing temperatures well below the incubation/control temperature of 37.8° C at the start of each rewarming period. Cold challenged embryos

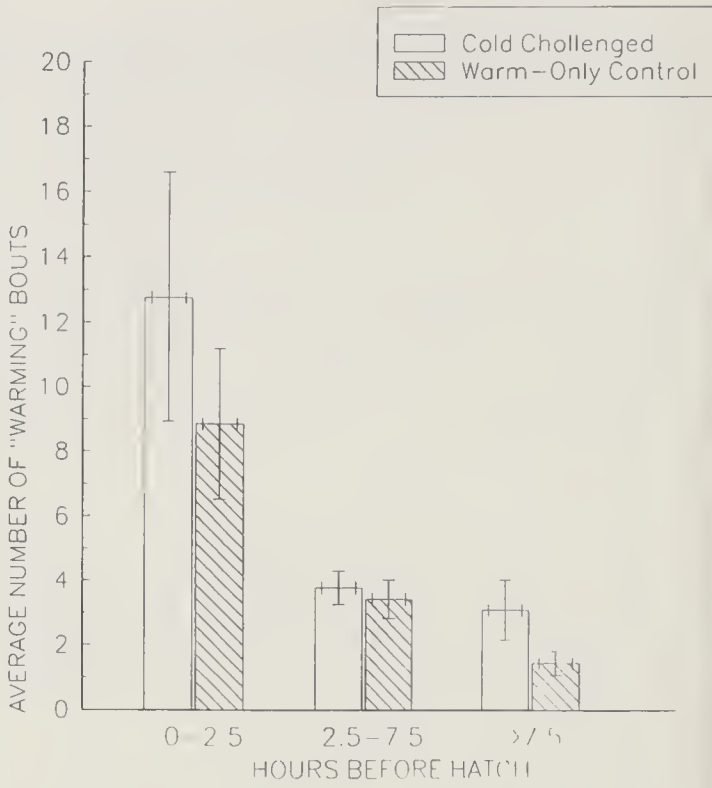

FIG. 1. Mean (±SE) number of vocally generated warming (cold challenged) and mock-warming (control) bouts at three pipped-egg developmental stages (cold challenge *n* equals 8, 13, and 12; warm-only control *n* equals 13, 12 and 9 for 0–2.5, 2.5–7.5 and >7.5 h before hatching respectively).

in the two groups vocalized more often than controls at this time, significantly so in the 2.5–7.5 h age group (Table 1). By the final minute of rewarming, the cold challenged embryos were almost silent, but this was also true for most of the control embryos whose temperatures had not changed. Control embryos that were less than 2.5 hours from hatch were an exception. These embryos vocalized at a relatively high rate during the final minute of the rewarming bout and maintained a call rate significantly greater than the experimental embryos.

Body temperatures maintained by experimental embryos during vocal regulation tests increased by about 1° C as hatching time approached, but this increase was not statistically significant (Fig. 1, Table 2). Body temperatures of experimentals were significantly lower than those of control embryos held at 37.8° C (Table 2), reflecting the general low level of call-induced rewarming periods in the experimentals. Body temperature of the experimental embryos by the end of 30 min of testing was significantly higher (29.9 ±

TABLE 1. Median number of calls per minute given by chicken embryos in pipped eggs at the start and end of vocally-generated rewarming (experimental) and mock rewarming (control) bouts. Listed are medians of calls given per embryo per bout (1st and 3rd quartiles in parentheses).

Stage (h before hatch)	First 20 s		Final minute	
	Experimental	Control	Experimental	Control
<2.5	9.6 (6.1–11.8)	6.6 (2.0–17.4)	0.2 (0.0–2.2)	3.1 (1.0–8.7)[a]
	$n = 8$	$n = 12$	$n = 8$	$n = 12$
2.5–7.5	9.0 (4.7–13.1)	3.0 (0.0–6.9)[a]	0.0 (0.0–1.4)	0.5 (0.0–2.3)
	$n = 12$	$n = 11$	$n = 12$	$n = 11$
>7.5	3.0 (1.7–5.3)	3.0 (0.0–6.0)	0.0 (0.0–0.5)	0.0 (0.0–0.5)
	$n = 8$	$n = 7$	$n = 8$	$n = 7$
H[b]	7.03	3.61	1.13	10.67
df	2	2	2	2
P	<0.05	>0.05	>0.05	<0.01

[a] Experimentals and controls differ significantly ($P < 0.05$: Mann–Whitney U test).
[b] H, Kruskal–Wallis ANOVA statistic, distributed as χ^2.

0.4° C, all stages combined; $t = 2.28$, $P < 0.05$, df = 23) than embryos that were exposed to constant chilling for 30 min in experiment 1 (28.8 ± 0.3° C). This suggests a slight warming effect of vocalizations in experiment 2.

DISCUSSION

Exposure of chicken embryos to continuous cold (20° C) and continuous hot (45° C) environments did not significantly increase their rates of vocalization. The embryos remained relatively silent in spite of exposure to environmental temperatures that altered body temperature to a level which, if continued, would be expected to result in death of the embryo (Webb 1987). While the embryos were clearly capable of vocalizing, the close correspondence of calling and temperature suggested in the literature (e.g., Collias 1952) was not evident. Only two cold challenged embryos, in the process of ringing prior to hatching, showed a strong vocal response. The vocal regulation experiments also showed an increase in vocal response in chilled embryos that were near to hatching (Fig. 1) but this trend was also seen in control embryos that were not exposed to cold. Tuculescu and Griswold (1983) have also noted a general increase in the rate of vocalization in the few hours just prior to hatching.

Despite increased vocalization rates as hatching approached, cold challenged chicken embryos in the vocal regulation apparatus were not able to elevate their body temperatures to safe, near normal incubation temper-

TABLE 2. Median body temperature of chicken embryos during experimental and control vocal regulation test. Listed are medians of the average body temperature maintained during the one-hour test period (1st and 3rd quartiles in parentheses).

Stage (h before hatch)	Body temperature of embryos (°C)		
	Experimental	Control	P[b]
<2.5	31.5 (30.0–35.5)	37.8 (37.2–38.0)	<0.002
	$n = 7$[a]	$n = 7$[a]	
2.5–7.5	30.5 (30.0–31.0)	38.1 (37.8–38.3)	<0.001
	$n = 13$	$n = 12$	
>7.5	30.4 (29.4–30.1)	37.6 (36.9–38.1)	<0.001
H[c]	$n = 12$	$n = 9$	
df	2.79	4.61	
P	2	2	
	>0.05	>0.05	

[a] Excludes 1 experimental and 6 control embryos that displaced the thermocouple during ringing.
[b] Comparison of experimentals and controls at each stage—Mann–Whitney U test.
[c] H, Kruskal–Wallis ANOVA statistic, distributed as χ^2.

ature, at least under the conditions employed here (Table 2). This contrasts strikingly with a significant increase in vocal regulatory capability of hatched domestic chicks given 2 min periods of rewarming in response to cold-induced calling on the day of hatching (Bugden and Evans 1997). The finding that body temperature after 30 min of testing of vocal regulation in 20° C cold challenged embryos was significantly different than cold only exposed embryos in experiment 1 is consistent with the presence of some incipient effects of vocally elicited rewarming bouts. Our results thus raise the possibility that the marginally higher rate of calling in cold challenged embryos, especially as they neared hatching (Fig. 1), may represent the beginnings of a prehatch vocal thermoregulatory response to cold.

Examination of the patterns of calling (Table 1) suggests that immediately before hatch (<2.5 h), rewarming was associated with decreased calling in experimental (cold challenged) embryos, while the calling of control embryos during the final minute of the 2 min mock rewarming period continued at a significantly higher level. This difference is also suggestive of an incipient vocal response to temperature by chick embryos during the final hours before hatching. An increase in vocal response to temperature as the time of hatching approaches has also been noted during vocal regulation studies in semiprecocial Ring-billed Gulls (*Larus delawarensis*; Evans et al. 1994) and Herring Gulls (*Larus argentatus*; Evans et al. 1995).

The subtle beginnings of the vocal response to temperature found here parallels the incipient development of endothermy in late stage chicken embryos. The prehatching endothermic response is not robust. It has been noted only when exposure to cold was limited to gradual cooling of late stage embryos (Tazawa et al. 1988). Incipient endothermy is thought to be limited initially by conductance of O_2 through the eggshell (Tazawa et al. 1989) and then by the embryo's limited endothermic power (Tazawa et al. 1988, Whittow and Tazawa 1991). While these physiological results suggest that incipient endothermy occurs during the latter stages of embryonic development, the dramatic increase in oxygen consumption at the time of hatching (Kuroda et al. 1990, Whittow and Tazawa 1991) indicates that endothermy becomes functional at that time (Freeman 1971, 1983). Our present results suggest that there is a similar incipient vocal thermoregulatory response of late stage embryos to cold that becomes fully functional at or soon after hatching (Tuculescu and Griswold 1983, Espira and Evans 1996, Bugden and Evans 1997). The developmental onset of vocal and metabolic thermoregulation thus appear to be closely linked in precocial domestic chicks.

In contrast to domestic chicks, the vocal thermoregulatory system of altricial pelicans and semiprecocial gulls is well developed prior to hatch (Evans 1988a, 1990a; Evans et al. 1994, 1995). Altricial and semiprecocial species evidently do not show any endothermic response before hatch (Matsunaga et al. 1989, Kuroda et al. 1990, Whittow and Tazawa 1991) suggesting that behavioral and metabolic thermoregulation are developmentally uncoupled in these species, unlike the apparent linkage in the domestic chicken.

Pelicans and gulls both exhibit asynchronous hatching, and later hatching eggs potentially experience significant levels of incubation neglect as the parents attend to the chicks that have already hatched (Evans 1990d, Lee et al. 1993, Evans et al. 1995). Although chickens display some level of hatching asynchrony (mean of 15 h in Burmese Junglefowl; Meijer and Siemers 1994), the chicken is not known to neglect its eggs and will normally remain on the nest for the first 12–24 h after hatching (McBride et al. 1969, Miller 1978, Meijer and Siemers 1994). A vocal response to cold thus may not be a functionally useful behavioral response for chicken embryos. After hatching, the situation changes dramatically when mobile chicks are potentially exposed to colder ambient temperatures, especially during foraging bouts (McBride et al. 1969, Sherry 1981). At that time calling to solicit brooding warmth becomes an important part of their behavioral response to cold (Kaufman and Hinde 1961, McBride et al. 1969, Sherry 1981). Taken together, results to date suggest that in precocial chickens, vocal and endothermic thermoregulation both show incipient, but largely nonfunctional, development prior to hatching and are both turned on rapidly as the chicks hatch and thermoregulation becomes a highly adaptive capability.

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BEHAVIOR AND VOCALIZATIONS OF THE CAURA AND THE YAPACANA ANTBIRDS

KEVIN J. ZIMMER[1,2]

ABSTRACT.—The first detailed information on the vocalizations (including the first sound spectrograms) and natural history of the Caura Antbird (*Percnostola caurensis*) and the Yapacana Antbird (*Myrmeciza disjuncta*) are presented. The Caura Antbird was studied in the Serrania de la Cerbatana, edo. Bolívar, Venezuela, where it inhabits humid foothill forest dominated by large rocks. Caura Antbirds specialized in foraging on or beneath rocks, a behavior unusual among the Thamnophilidae. The Yapacana Antbird was studied at a site along the south bank of the Río Ventuari, edo. Amazonas, Venezuela. These antbirds were locally abundant in a specialized stunted woodland that grows on white sand soils. Based on newly described vocal characters, the closest relatives of *P. caurensis* appear to be *P. leucostigma* and *P. schistacea*, whereas *M. disjuncta* has no apparent close relatives and probably merits placement in a monotypic genus. *Received 9 July 1998, accepted 5 Jan. 1999.*

Among the least known members of the large antbird family Thamnophilidae are the Caura Antbird (*Percnostola caurensis*) and the Yapacana Antbird (*Myrmeciza disjuncta*). Both species are nearly endemic to southwestern Venezuela and have remained relatively unobserved by modern field ornithologists. The most extensive collections of both species (36 specimens of *P. caurensis* and 5 specimens of *M. disjuncta*) reside in the Colección Ornitológia Phelps (COP), Caracas, Venezuela. Single specimens of each species collected near Pico Neblina (edo. Amazonas, Venezuela) in 1984 by Field Museum of Natural History (FMNH) personnel represent the only specimens of *P. caurensis* and *M. disjuncta* collected anywhere since 1972 and 1981 respectively. There is essentially no published information on habitat or behavior of the two species, and nothing is known of their vocalizations (Ridgely and Tudor 1994).

In February 1998 I observed the habitats and behaviors and tape-recorded the vocalizations of Caura Antbirds in the Serrania de la Cerbatana, edo. Bolívar, Venezuela, and of Yapacana Antbirds in Yapacana National Park, edo. Amazonas, Venezuela. This is the first detailed information on the natural history and vocalizations of these species and allows a more informed assessment of their possible generic affinities.

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STUDY AREAS AND METHODS

I observed Caura Antbirds 10–15 February, 1998 in the Serrania de la Cerbatana near Hato Las Nieves (6° 34′ N, 66° 12′ W), edo. Bolívar, Venezuela (Fig. 1). The Serrania de la Cerbatana rings a large valley vegetated mostly by a mixture of savanna and tropical dry forest, transected by narrow bands of gallery forest along occasional streams, and dotted with groves of *Mauritia* palms in poorly drained areas. Three main rivers, Caño Las Nieves, Río Agua Fria, and Río Danta, drain the valley. The Serrania mountain range rises dramatically from the valley, and on the southern and western borders is covered with humid forest. The south facing slopes of the mountains to the north of the valley are noticeably drier. The tallest peak in the chain is Pico Las Nieves at 2080 m. I studied Caura Antbirds along a 1.5 km trail that began in humid forest at 280 m elevation and extended up the side of a ridge to 400 m.

I studied Yapacana Antbirds 22–27 February 1998 along a trail (hereafter the "Picua Trail") near the settlement of Picua (4° 5′ N, 66° 45′ W) in Yapacana National Park, edo. Amazonas, Venezuela (Fig. 1). Picua is a small settlement of Piaroa and Mako Indians, on the south (left) bank of the Río Ventuari at about 150 m elevation. The surrounding area contains a mosaic of different soil types that support a patchwork of distinct vegetation types. The Ventuari and its many small tributaries are flanked by bands (of varying width) of tall forest (15–25 m) that grow on yellow clay soils and are seasonally flooded. This várzea forest is characterized by a closed canopy with a fairly open understory and an abundance of vines and lianas. On higher banks above the river the várzea grades into a taller transitional forest with a denser understory. Much of the area farther removed from the river is dominated by white sand soils on which grow lower stature woodlands and grassy savannas. The savannas range in size from less than 1 ha to about 1 km^2, with scattered shrubs and small trees. Larger savannas in the area contained stands of *Mauritia* palms. Large, isolated patches of red clay soils support tall (>30 m),

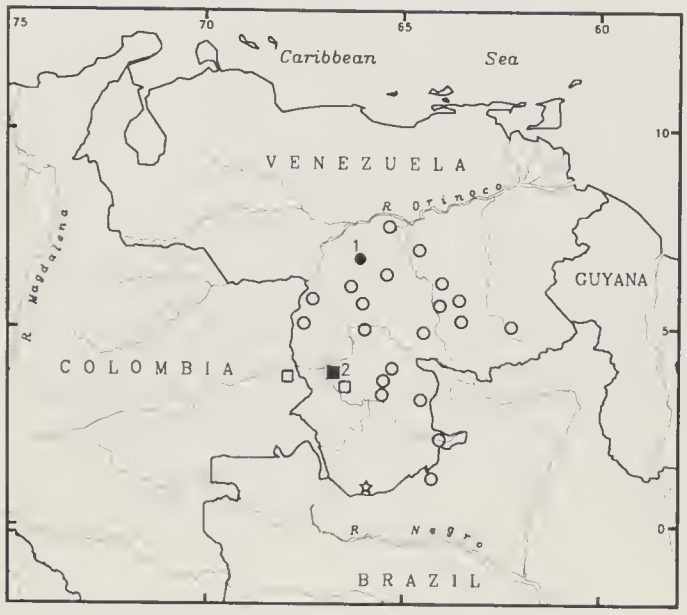

FIG. 1. Distributions of Caura Antbird (*Percnostola caurensis*) and Yapacana Antbird (*Myrmeciza disjuncta*): open circles = confirmed sites for *P. caurensis* (confirmation based on specimen records); open squares = confirmed sites for *Myrmeciza disjuncta*; open star = site near the base of Pico de la Neblina where both species have been collected in close proximity. The black circle and #1 indicates the site of the present study in the Serrania de la Cerbatana, edo. Bolívar, Venezuela where *P. caurensis* was studied. The black square and #2 indicates the site of the present study near Picua, in Yapacana National Park, edo. Amazonas, Venezuela where *M. disjuncta* was studied.

lush "islands" of humid tropical forest that are not seasonally flooded (= terra firme forest). Quartzite dome-like sandstone hills (cerros) and low outcroppings are scattered throughout the region.

Whenever individuals or pairs of *P. caurensis* or *M. disjuncta* were located, I followed them for as long as possible, tape-recording as many vocalizations as I could and summarizing foraging and other behaviors on cassette tape. Some of these behaviors were also documented on videotape. I used tape-playback of these recordings to assess presence or absence of antbirds in places where no spontaneously vocalizing birds were heard and to determine the limits of territorial boundaries. All measurements included in such summaries (height above ground, territory size, distances, times, etc.) are estimates. Terminology for foraging behavior follows Remsen and Robinson (1990).

Tape recordings were made with a Sony TCM-5000 recorder and Sennheiser MKH-70 microphone. All recordings have been or will be archived at the Library of Natural Sounds, Cornell Univ., Ithaca, New York. Spectrograms were made by Phyllis Isler on a Power Macintosh 7500 computer using Canary version 1.2.1 (Bioacoustics Research Program, Cornell Laboratory of Ornithology, Ithaca, New York). Morton Isler compiled a comprehensive list of distributional records of the two species of antbirds as documented by specimens, tape recordings, or photographs (Isler 1997; Fig. 1).

PERCNOSTOLA CAURENSIS

Distribution and habitat.—The Caura Antbird is known only from the western portion of the "Pantepui" region (Mayr and Phelps 1967) south of the Río Orinoco in the Venezuelan states of Bolívar and Amazonas and in extreme northern Brazil (Fig. 1). *Percnostola caurensis* is well represented in museum collections, with 36 specimens (the most recent collected in 1972) in the Coleción Ornitológia Phelps (Caracas, Venezuela) alone (C. Rodner, pers. comm.). The most recent substantiated record was of a male collected in 1984 at 1250 m near the base of Pico Neblina (edo. Amazonas, Venezuela; Willard et al. 1991). The occurrence of *P. caurensis* in the Serrania de la Cerbatana represents a slight range extension to the northwest (Fig. 1).

The forest along the first 500 m of the trail was tall (ca 30 m), with an open understory dominated by slender palms. The terrain was flat and nearly devoid of large rocks. I could locate only one territory of *P. caurensis* along this portion of the trail, and it abutted the bottom of the hill. The hillside forest beyond 500 m was also fairly open, with an intermittent canopy of about 20 m. Few trees were larger than 30 cm dbh, and woody vines were abundant. Large stands of a narrow-leaved, non-spiny bamboo (1–2 m in height) occupied most light gaps. The entire slope was extremely rocky, with numbers of boulders up to 8 m tall and 15 m along their longest axis. These boulders were typically moss and fern covered, with terrestrial bromeliads, cacti, and bamboo growing over their tops and in the crevices (Fig. 2). Many were topped with small trees, the gnarled roots of which draped off the sides of the rocks like tendrils, trapping leaf litter and organic debris. I located 6 pairs of *P. caurensis* along about 1 km of trail through this rocky, hillside forest.

The Serrania de la Cerbatana was extremely dry in February 1998. Typical dry season conditions appeared exacerbated by ongoing El Niño related events. Leaf litter throughout the forest was extremely dry and many trees had shed large numbers of leaves. This was particularly evident in the hillside forest, where large patches (0.5–1 ha) of deciduous vege-

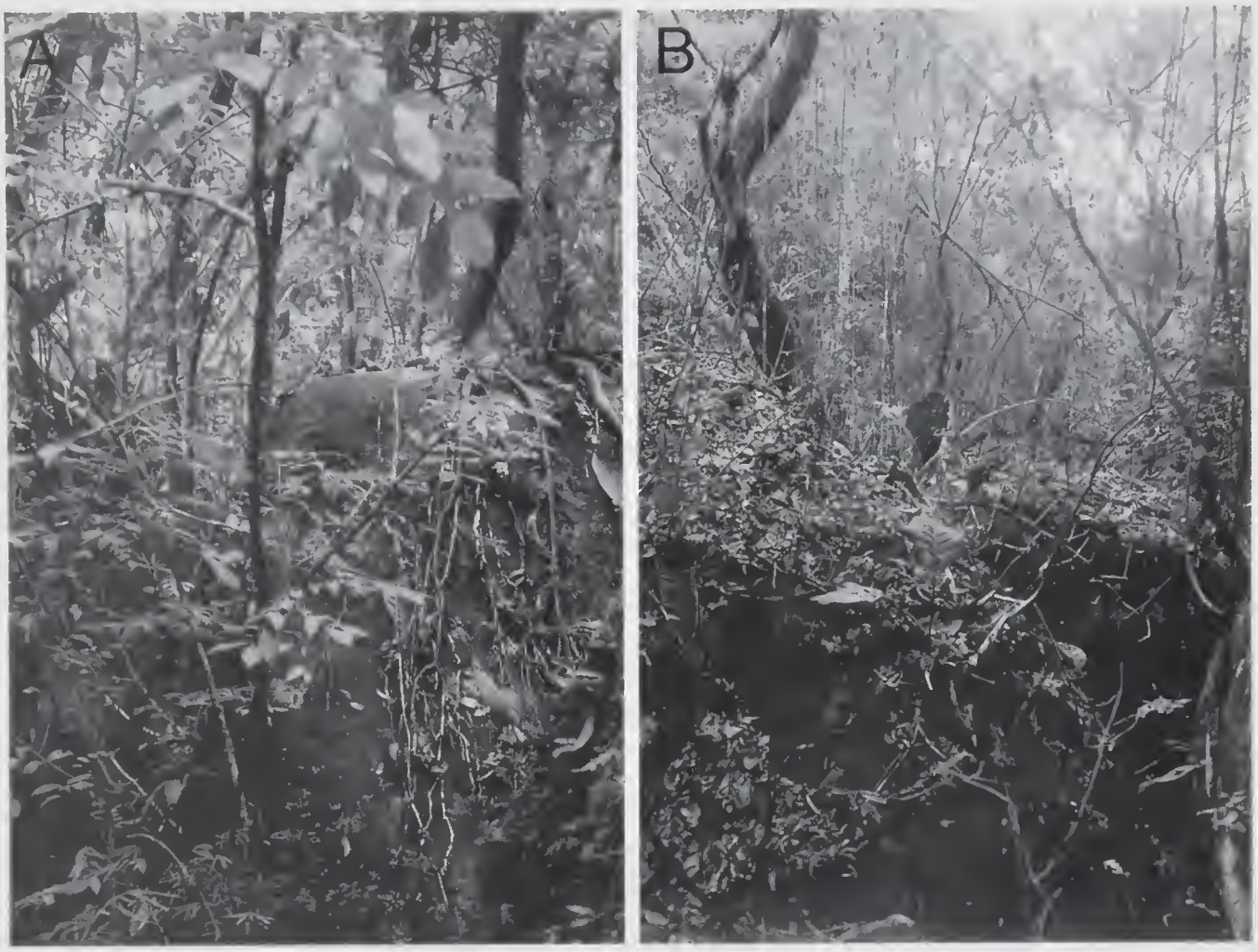

FIG. 2. Rocky hillside forest in the Serrania de la Cerbatana, edo. Bolívar, Venezuela. (A) Relatively open forest, with a broken canopy of about 20 m. The rocks were 2–3 m tall and 4 m in diameter. (B) A rocky alluvial fan along which were located two Caura Antbird territories. Note the highly deciduous state of the vegetation in this light gap, and the abundance of leaf litter trapped in the roots and vines overtopping the rocks.

tation were conspicuously scattered across the slope, usually coincident with the rock strewn alluvial fans at the bottom of ravines.

Morphology.—Soft-part colors were identical for both sexes. The iris was reddish-brown, the legs and feet were slate gray (a shade paler than the bill), and the bill was blackish. Plumage was as described by Ridgely and Tudor (1994).

Vocalizations.—Caura Antbirds were generally quiet during my fieldwork, as were most other species of insectivorous birds. Dawn choruses were both unremarkable and short, suggesting a low level of breeding activity for most species during the height of the dry season. There was a sustained rain during the early morning hours of 13 February; the two following mornings I noted increased spontaneous song from Caura Antbirds.

I recorded over 120 loudsongs (as defined by Isler et al. 1997) and 900 calls from 12 individual antbirds. The loudsong of *P. caurensis* is a far carrying series of 7–15 modulated and well spaced notes (Fig. 3A). The first notes are widely spaced, and the terminal notes are closer together and drop in pitch. Female songs (Fig. 3B) were similar in pattern to male songs, but differed in other characteristics such as mean number of notes, mean frequency, etc. Females sang less frequently than males.

In response to tape playback and during territorial encounters, both sexes gave loud, buzzy "zhew" calls at varying levels of frequency modulation (Figs. 3C–E). On a few occasions, birds involved in territorial disputes uttered sharp "quip" notes (Fig. 3F) when neighboring birds approached closely. The most frequently heard vocalization, and one given by birds startled along the trail, was an abbreviated loud rattle (Figs. 3G, H), similar to the alarm calls of *P. leucostigma* and

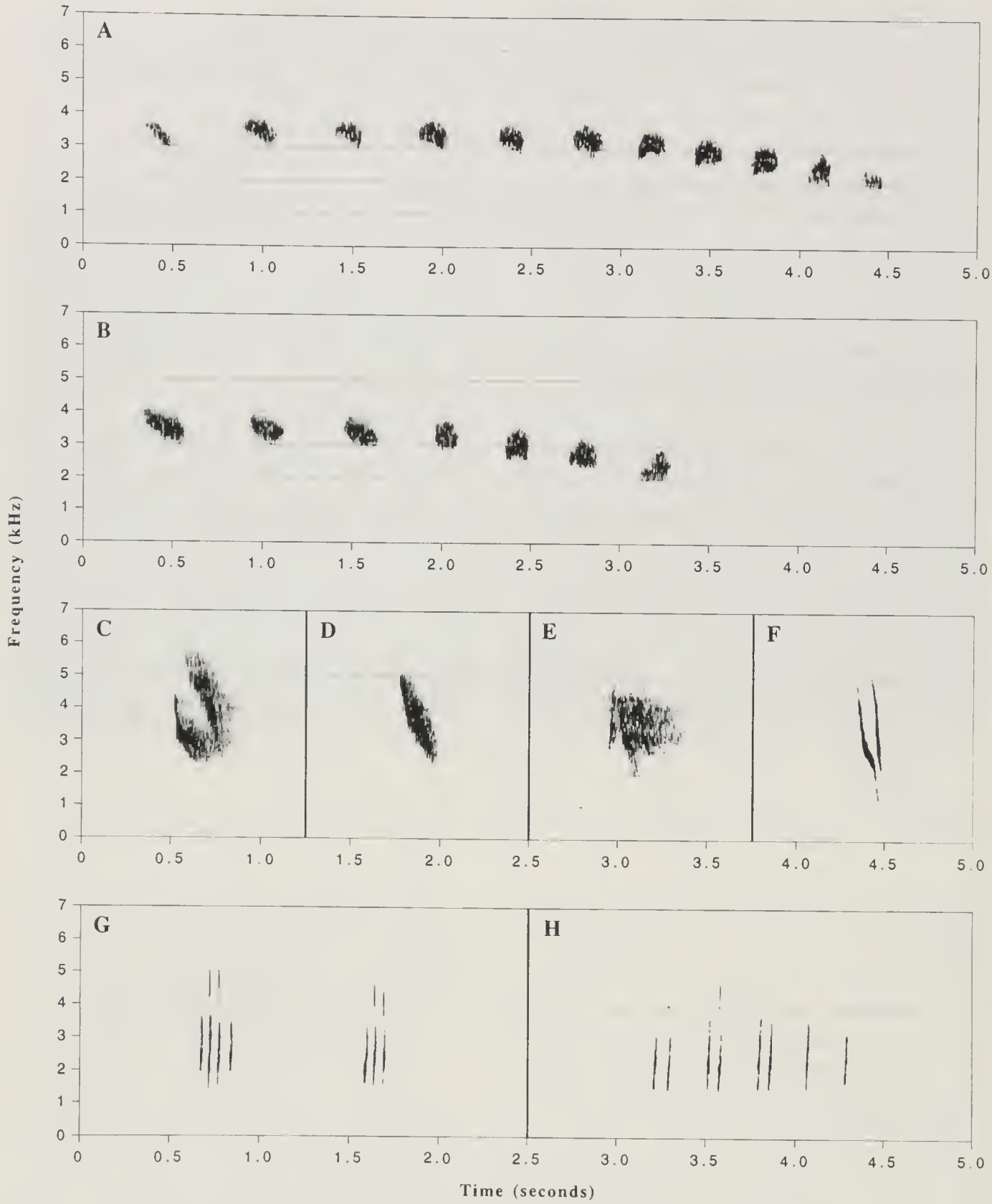

FIG. 3. Spectrograms of Caura Antbird (*Percnostola caurensis*) vocalizations: (A) male loudsong, (B) female loudsong, (C, D, E) "zhew" calls, which probably function as aggression calls, at various levels of frequency modulation, (F) "quip" call, (G) male alarm rattles, and (H) female alarm rattles.

several species of *Myrmeciza* antbirds (pers. obs.). A loud "chikit" (not tape recorded) was often given by Caura Antbirds at the moment they took flight. Birds alarmed by my presence gave this call immediately before flushing, as did birds chasing one another about in an aggressive boundary dispute.

Behavior.—Caura Antbirds were encoun-

tered singly or in pairs, but did not associate with mixed-species flocks. Mates foraging together were typically within 15 m of one another, and alarm calls from one bird elicited an immediate vocal response from the other. Foraging birds maintained a nearly horizontal posture, with the head held higher than the axis of the body. All individuals continuously raised their tails a few degrees above the plane of the body and then wagged them slowly downward in an arc 20–30° below the plane of the body. This tail movement was most exaggerated when the antbirds clung laterally to elevated perches or responded to tape playback, but was also used during terrestrial foraging. Mostly the tail appeared to be slightly fanned. Tail movements were occasionally accompanied by a simultaneous wing-flick.

Caura Antbirds foraged mostly on rocks or the ground. Both sexes spent long times creeping over the large boulders, often clinging laterally to nearly vertical rock faces and going in and out of the numerous crevices (often for minutes at a time) in the manner of Slaty Bristlefronts (*Merulaxis ater*; M. Isler and P. Isler, pers. comm.), Rock Wrens (*Salpinctes obsoletus*) or Canyon Wrens (*Catherpes mexicanus*). While creeping about the rocks, the antbirds frequently probed in the mosses and small ferns covering the surface, but spent most of their time inspecting the leaf litter trapped between the roots and vine tangles of trees overtopping the boulders. Arthropod prey (primarily orthopterans and hemipterans, as well as many arthropods too small to be identified) were gleaned from root and vine surfaces with quick stabbing motions. Curled dead leaves were carefully probed with the bill. Some antbirds inspected dead leaves without tossing them, others picked up leaves with the bill before tossing them aside. The antbirds routinely squeezed themselves into small spaces between the rock surface and overlying roots and vines, remaining in these somewhat "canopied" niches to forage for up to 60 s. When foraging on rocks, the antbirds tended to spend most of their time in somewhat protected locations, within the interior of vine tangles and root masses overtopping the rocks, within crevices in the rocks, or beneath rocky ledges and overhangs. The antbirds moved steadily over open rock faces, progressing by short hops of 5–10 cm and occasional longer wing-assisted hops or short, abrupt flights, often to low, overhanging branches or ledges. They frequently hopped from a rock up to a low branch or sapling to scan for 1–5 s before dropping back to the rock. Birds often dropped 1–5 m from the rocks to the ground. There, they hopped beneath the overhangs, probed in leaf litter and inspected rock surfaces. Antbirds spent many minutes inspecting fissures, crevices, and gaps within and between rocks, often retracing their routes.

One male observed foraging for more than 30 minutes spent the bulk of this time foraging over, under, and between rocks, probing in moss and vine tangles. On three occasions the bird dropped to the ground at the base of large rocks and spent 1–5 minutes vigorously tossing dead leaves in the manner of a leaftosser (*Sclerurus* spp.). Large leaves (many larger than the bird) were picked up with the bill and tossed. Smaller leaves were frequently flipped by inserting the bill beneath the leaf and then giving a quick upward flaking motion. He also made an upward sally of 20–25 cm from the ground to take an unidentified arthropod from the underside of a green leaf. Other individuals occasionally made similar short upward sallies to glean prey from overhanging rocks.

One female antbird spent several minutes hopping around the periphery of a large emergent swarm of small, winged ants. Although she picked at the ground several times, it was not clear whether she was feeding on the ants. The bird flew off and returned to the ant-swarm twice. The male antbird was foraging nearby, but did not attend the swarm.

Territories appeared to be about 150–200 m in diameter. I witnessed only one territorial conflict. This was a prolonged encounter between pairs whose territories bounded a large rock-slide along the center of a ravine. The conflict was marked by several advances and retreats by both pairs. Both members of each pair countersang at length while gradually approaching their counterparts. Whenever the pairs approached to within about 20 m of one another, they tended to substitute "zhew" calls for songs. When they were in visual contact or close auditory contact, the pairs exchanged harsh calls for a few minutes before one individual or pair retreated, often with its rival in close pursuit. These abrupt retreats

were always preceded by the loud, hard "chikit" call. The dispute lasted for more than 30 minutes. Eventually the pairs retreated to opposite ends of the rockslide, periodically singing.

Most species of passerines besides *P. caurensis* were encountered in mixed-species canopy and mid-level flocks. The apparent absence of terrestrial or semi-terrestrial antbirds (other than *P. caurensis*) or furnariids is noteworthy, although my failure to detect such species could be an artifact of depressed song activity during the dry season. The taller, less-deciduous forest below the mountains had a more diverse avifauna.

The presence of large rocks appeared to be a critical component of *P. caurensis* habitat. Of the 7 territories, 6 were in areas with abundant large rocks. The seventh territory was close enough to the bottom of the hillside to possibly have included some rocky terrain as well. The rocks provided microhabitats in which a diversity of plants flourished, and these plants, in turn, provided a wealth of potential foraging strata for a small terrestrial insectivore such as *P. caurensis*. Caura Antbirds spent more than 80% of their foraging time on rocks and overtopping vegetation, or on the ground directly beneath overhanging rocks. The importance of rocks as foraging sites for Caura Antbirds may be increased during the dry season, when favorable moisture-retaining microclimates are created along rock edges or crevices. Furthermore, the tendency for overtopping root masses and vine tangles to trap leaf litter is accentuated during the dry season, when many trees drop their leaves. Such accumulations of organic litter may provide attractive sites for arthropods when the forest is water-stressed. It is interesting that no other bird species was observed to exploit the extra resource dimensions created by the large rocks. The presence of Guianan Cock-of-Rock (*Rupicola rupicola*) in the area is almost certainly dependent on the availability of large rocks for nest sites (Snow 1982), but only the Caura Antbirds seemed to use the rocks as foraging substrates.

MYRMECIZA DISJUNCTA

Distribution and habitat.—The Yapacana Antbird was described in 1945 by H. Friedmann from two specimens collected near the base of Cerro Yapacana (edo. Amazonas, Venezuela) in April 1931. Five more specimens were collected from the same general locality in April–May 1947 (specimens COP). Cerro Yapacana is an isolated outlier of the western Tepuis, rising steeply above the Río Orinoco to an elevation of 1340 m. Meyer de Schauensee and Phelps (1978:218), perhaps describing the general habitat surrounding Cerro Yapacana, listed the habitat of *M. disjuncta* as "High rain forest at about 100 m in undergrowth and low bushes." Subsequent to its description, *M. disjuncta* has been documented from only three additional sites (Fig. 1). In March 1981, while working in sandy-belt forest near Puerto Inírida, depto. Guainía, Colombia, J. Dunning mist-netted an antbird later identified from photos as a female Yapacana Antbird (Hilty and Brown 1986; ANJP specimen 175723, R. Ridgely, pers. comm.; photo on file at VIREO). In February 1984 a single female *M. disjuncta* was collected at 140 m near the left bank of the Río Baría on the Venezuelan-Brazilian border (Willard et al. 1991). This extended the known range of *M. disjuncta* about 350 km south. There is no published description of the habitat in which this Yapacana Antbird was collected, but the nearby base camp was in "tall seasonal rain forest drained by both black-water and white-water streams" (Willard et al. 1991). J. Coons and D. Stejskal (pers. comm.) were the first to find *M. disjuncta* near Picua in January 1997. They reported seeing or hearing several individuals in savanna woodland on white sand soils along the Picua Trail.

The only habitat of the Ventuari in which I found *M. disjuncta* was what the local people refer to as "monte cerrado." I found this habitat only on the south bank of the Río Ventuari along the Picua trail. This is a stunted, virtually impenetrable woodland that grows on fine, compacted white sand soils that are seasonally saturated (Fig. 4). It is similar to the "savanna woodland" described from Campamento Junglaven located farther north (upstream) along the Ventuari (Zimmer and Hilty 1997) but has a greater density of vines, along with abundant sawgrass and bamboo scattered through the understory. The canopy varies from 6–10 m and is of generally uniform height with only occasional emergent trees of

FIG. 4. (A) Monte cerrado woodland along the Picua Trail, Yapacana National Park, edo. Amazonas, Venezuela. (B) Interior of the monte cerrado, depicting a typical Yapacana Antbird territory.

10–15 m. Few trees in this habitat have trunks thicker than 10 cm dbh.

A different type of "sandy belt forest" or savanna woodland occurred on the north bank. This woodland was partly deciduous, less diverse, and even more stunted than the monte cerrado. The understory was more open and lacked both bamboo and sawgrass. This forest grew on coarser, well-drained white sand soils atop low ridges or rocky outcroppings. *Myrmeciza disjuncta* and many other species typical of the monte cerrado were absent from this scrub woodland.

Using tape playback I located at least 24 pairs of *M. disjuncta* along 1350 m of the Picua Trail. No birds were detected farther than 50 m from the trail. Territories were evenly spaced along both sides of the trail and appeared to be no more than 50–75 m in diameter. Near the savanna edge the monte cerrado was particularly stunted, with a more open canopy and more sawgrass in the understory. I found only two territories of Yapacana Antbirds along more than 150 m of trail transecting this more grassy woodland.

Morphology.—There has been some confusion in the literature regarding plumage characters of *M. disjuncta.* Central to the confusion is the type specimen of *M. disjuncta,* an immature male molting into adult plumage (Friedmann 1945, 1948), which displayed a combination of adult and immature plumage characters. Thus, Meyer de Schauensee (1970: 249) wrote that the male has "upperparts blackish-gray, crown and nape tinged brown" and "sides of head gray, chin white; rest of underparts white, strongly tinged ochraceous buff; center of abdomen white." Similarly, Meyer de Schauensee and Phelps (1978:218) described the male plumage as having the "throat and breast white suffused with ochraceous tawny, strongly so on breast and sides of throat, middle of abdomen white, undertail coverts dark gray." They described the female as differing from the male by "dark ochraceous buff spots on wing coverts and ochra-

ceous under tail coverts." This description was essentially repeated in Hilty and Brown (1986). Ridgely and Tudor (1994:332) were much more nearly correct in both their illustration of the male and in the description of the plumage, but still suggested that the underparts of the male are "tinged with creamy buff."

None of the 20 or more male Yapacana Antbirds that I saw showed any hint of tawny, ochraceous buff, or creamy buff color on the underparts, nor did they have the crown or nape tinged brown. Instead they were uniformly dark gray (with an almost steely blue cast) above (except for the usually concealed white interscapular patch) and on the sides of the face, with the chin, throat, breast, belly, and undertail coverts white. The sides and flanks were washed with gray, but these areas were often concealed by the wings. The wing coverts were blackish, with the lesser and median wing coverts fringed white. The tail was blackish and the rectrices were either narrowly tipped or fringed white. This character is not mentioned in any of the previous descriptions, possibly because the narrow white tips/fringes were lost to wear in the few existing specimens. The legs were pinkish gray, the iris blackish brown, the maxilla blackish, and the mandible whitish. Females differed in having a slightly brownish cast to the upperparts, particularly the crown and nape, which contrasted with the gray sides of the face. The underparts were a bright ochraceous buff (almost pale orange) from the throat to the undertail coverts, and were only slightly paler on the chin and upper throat. I did not note pale tips or fringes on the rectrices of females, nor could I confirm the presence of a contrastingly colored interscapular patch.

All birds that I saw had proportionately short, broad tails that appeared graduated. This could have been influenced by molt, but, if so, all of the individuals in this area were highly synchronous in the regrowth of their outer rectrices.

Vocalizations.—J. Coons and D. Stejskal (pers. comm.) tape recorded some single-note harsh calls of *M. disjuncta* during their January 1997 visit to Picua, but did not encounter singing birds. Yapacana Antbirds were also generally quiet during the period of my field work. Even at dawn there was little spontaneous singing, suggesting that the level of breeding activity was low. However, birds were highly responsive to tape playback, which often elicited singing from one or more neighboring pairs in addition to the resident pair. Both males and females responded vocally to playbacks, although males were much more aggressive in approaching the speaker. All types of vocalizations that I recorded were given by both sexes of Yapacana Antbirds. I tape recorded over 350 loudsongs and 230 calls from 34 individuals.

The typical loudsong of *M. disjuncta* consisted of two prolonged, harsh, heavily frequency modulated notes separated by a short pause, into which were inserted one or two "pip" notes (Fig. 5A). The first harsh note was the longest, and increased in intensity while rising in pitch. The second harsh note was shorter and had a more uniform amplitude. A typical loudsong could be transcribed as "cchhhhhhh pipizhhhh". On many occasions birds sang songs with no discernible "pip" notes between the harsh elements, although spectrograms of such songs reveal a distinct spike at the beginning of the second harsh note (Fig. 5B). Less frequently birds sang songs with three harsh elements instead of two (Figs. 5C, D). The third harsh note in such series was usually the shortest. Loudsongs varied in duration, depending largely on the number of harsh elements included. I could find no consistent differences between male and female songs, although males more frequently inserted two "pip" notes between harsh elements and females more frequently sang songs with no "pip" notes.

The most commonly heard calls were long, harsh, single notes, at a somewhat higher pitch than the harsh elements of the song, and with a peculiar, slightly nasal quality (Figs. 5E, F). These "harsh calls" were given by both sexes, although those of females were higher pitched. "Harsh calls" seemed to be aggression calls given in response to tape playback or by a bird disturbed by my presence. Birds occasionally gave a soft rattle (Fig. 5G) in a similar context. When Yapacana Antbirds of either sex were suddenly startled or strongly agitated, they gave one or more sharp and somewhat squeaky "squip" notes (Fig. 6A). These notes were similar in tonal quality to the notes inserted between the primary harsh

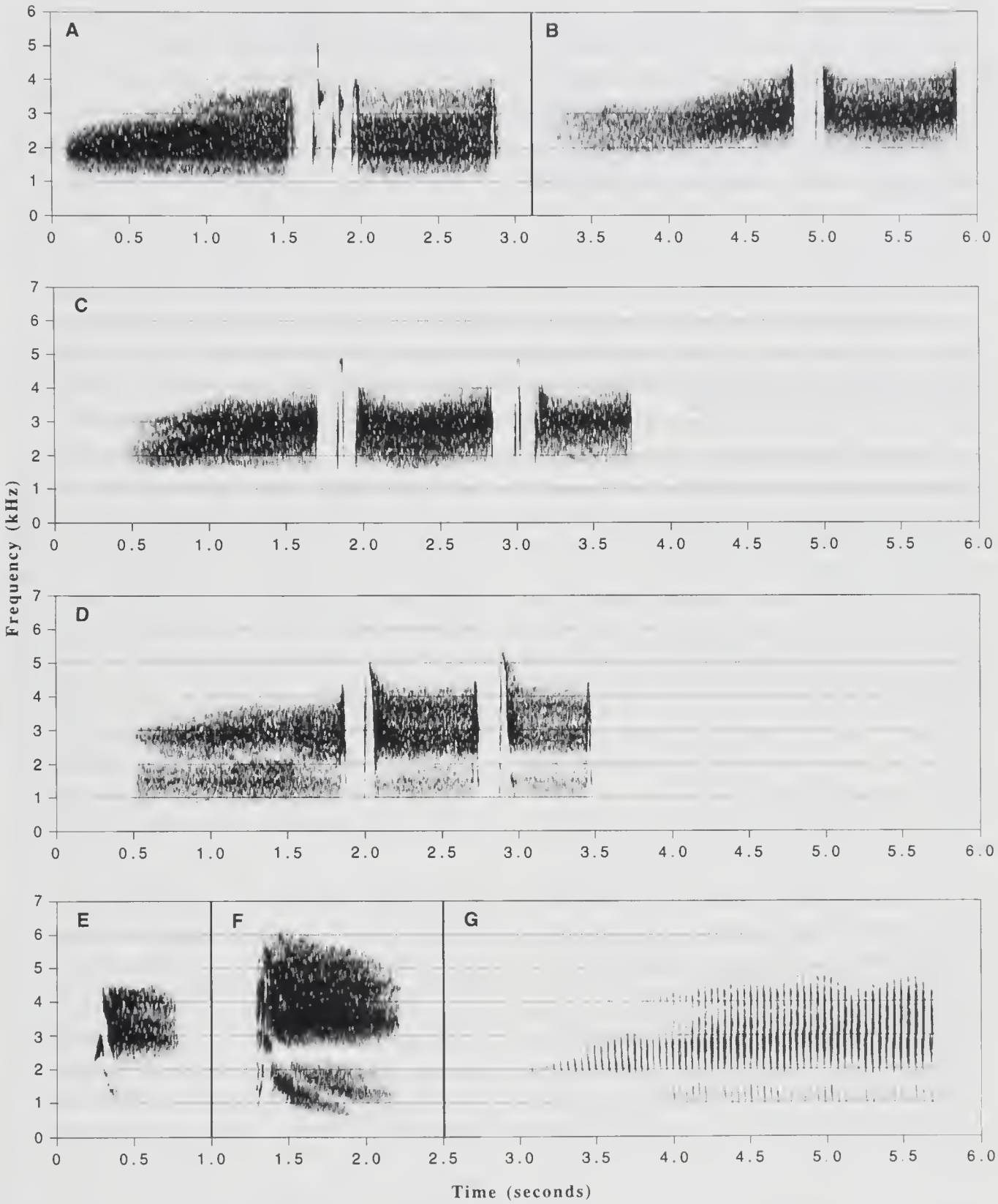

FIG. 5. Spectrograms of Yapacana Antbird (*Myrmeciza disjuncta*) vocalizations: (A) male loudsong with two "pip" notes inserted between the primary harsh elements, (B) loudsong variant with no discernible "pip" notes between harsh elements (sex of singing bird unknown), (C) loudsong variant with three harsh elements and single "pip" notes (sex of singing bird unknown), (D) loudsong variant with three harsh elements and no "pip" notes (sex of singing bird unknown), (E) male harsh call, probably an aggression call, (F) female harsh call, probably an aggression call, and (G) soft rattle call, given in an aggressive context.

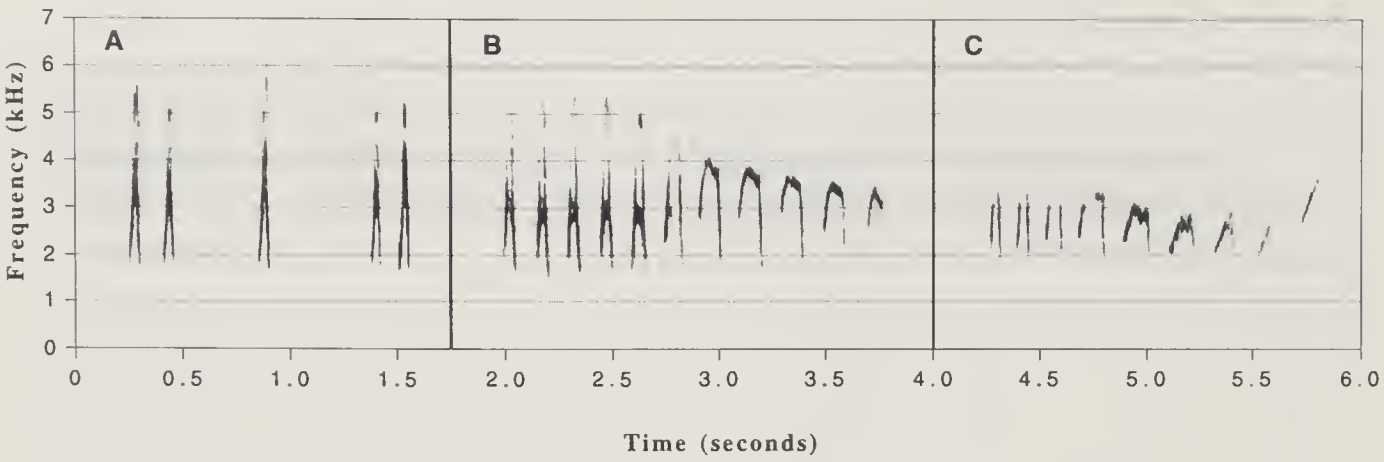

FIG. 6. Spectrograms of Yapacana Antbird (*Myrmeciza disjuncta*) calls: (A) "squip" notes given by a startled or alarmed bird, (B) rarely heard complex call (sex of calling bird unknown), and (C) variant complex call (sex of calling bird unknown).

elements of most loudsongs. Occasionally birds of either sex gave a more complex call that began with several "squip" notes and ended with a descending series of soft, whistled "wheee" or "whew" notes (Figs. 6B, C). These complex calls had a distinct tailing off quality, as in "squip squip squip wheee wheee wheee whew whew." The function of these calls was not clear.

Behavior and sociality.—Yapacana Antbirds were encountered singly or in pairs and did not associate with mixed-species flocks. Given the relatively small size of their territories, members of pairs were rarely far from their mates. An alarm call or song from one bird almost invariably brought an immediate vocal response from its mate. I did not witness any confrontations between neighboring pairs of antbirds, although on several occasions a singing pair of birds stimulated an adjacent pair to approach the apparent boundary and countersing for several minutes.

Yapacana Antbirds typically maintained a horizontal posture, with the head held higher than the axis of the body. Singing birds usually maintained a more upright posture. The tail was held within a few degrees above or below horizontal, and often was kept slightly fanned. Foraging birds often quickly flicked the tail up and down in a shallow arc of less than 10°, but just as frequently dipped the tail slowly downward at about a 30° angle before flicking it back up more rapidly. Singing birds frequently shivered the tail up and down more rapidly throughout a song. Some individuals wagged their tail sideways in a slow, somewhat jerky manner. Such motions involved the entire tail being swung a few degrees away from the axis of the body, held briefly in that position, then swung still further in the same direction before being swung back into alignment. This jerky motion is similar to some of the tail movements employed by the Silvered Antbird (*Sclateria naevia*; pers. obs.). Whether foraging or singing, Yapacana Antbirds flicked their wings at least once during virtually every pause between hops. Wing-flicks occurred both independent of and in synchrony with tail movements. Singing birds rarely sang consecutive songs from the same perch. In response to tape playback males often exposed a white interscapular patch.

Yapacana Antbirds foraged mostly on or near the ground, always lower than 1.5 m. They were restless, active foragers, moving by short hops (often wing assisted) and seldom pausing for more than 2 s in one spot. When moving above the ground they clung laterally to slender vertical saplings or perched across horizontal limbs and vines, progressed in an often erratic, zigzag course, and frequently moved up and down. They were adept at clinging to the thinnest stems, including slender bamboo stalks and vines. On a few occasions I saw birds hop headfirst down nearly vertical stems or branches, almost in the manner of a nuthatch (*Sitta* spp.). Birds frequently took several hops on the ground before jumping up to a low perch and then back down to the ground. Small arthropod prey were gleaned from stems and from tops and bottoms of live leaves by reaching out, up, or

down on extended legs and with neck craned. Prey were captured with a quick stabbing motion of the bill and swallowed entire. Larger prey items were bashed against the perch and mandibled one or more times before being swallowed. Antbirds typically wiped their bill on the perch after swallowing prey. Most prey items that could be identified were small orthopterans (katydids and crickets), hemipterans, and geometrid larvae.

I encountered Yapacana Antbirds foraging in the open along the main trail on only three occasions. Two of these encounters involved pairs, and the other involved a lone female plumaged bird. In each case the birds were working the edge of the dense monte cerrado vegetation, as well as shrubs and clumps of grass growing in parts of the trail. All foraged mostly on the ground, progressing by a series of short hops with minimal pauses in between, and always with wings (and frequently the tail) flicking. The most frequent attack maneuvers were gleans from the surface of the leaf litter or brief probes with the bill beneath the leaf litter. The next most frequent technique was reaching up to glean from the undersides of overhanging green leaves and grass blades. On several occasions birds jumped 6–15 cm upward to glean prey from the undersides of leaves. The two pairs of antbirds encountered in the open were found in the early morning before the sun had illuminated the trail. The lone female plumaged bird (possibly a subadult male) was found in midmorning, when the entire trail was sunlit and temperatures were already above 30° C. I followed this bird as it foraged steadily at the edge of the woodland for more than 20 minutes and covered more than 50 m. It crossed at least one known territorial boundary, but remained silent and did not attract attention from any other antbird.

On one occasion I found a female Yapacana Antbird attending a foraging swarm of army ants (*Eciton* sp.) within the monte cerrado. I observed this bird over 20 minutes during which it was the only bird attending the swarm. The female antbird employed two strategies in the vicinity of the ants. Part of the time she scanned the swarm from perches within 0.3 m of the ground, dropped to the ground to seize fleeing arthropods (orthopterans, hemipterans, and spiders) and then returned to a low perch to beat the prey on a branch before swallowing. Slightly more time was spent hopping on the ground between the columns of ants and tossing dead leaves in the manner of a leaftosser (*Sclerurus* spp.). Most leaves were tossed by inserting the bill beneath the leaf and lifting it with a quick flaking motion. Occasionally the bird picked up a leaf in its bill and tossed it aside. David Wolf (pers. comm.) observed another female antbird (away from ants) that remained in one spot tossing leaves in a similar manner for 1–2 minutes.

I observed no other species of terrestrial or semi-terrestrial antbirds in the monte cerrado. The Black-throated Antbird (*Myrmeciza atrothorax*) and the Black-chinned Antbird (*Hypocnemoides melanopogon*), both of which routinely forage below 1.5 m (Hilty and Brown 1986; pers. obs.), were locally common in nearby forest or edge habitats, but were not found in the monte cerrado. The only other passerine (besides *M. disjuncta*) in this habitat that I found foraging below 1.5 m was the Buff-breasted Wren (*Thryothorus leucotis*), which foraged everywhere from the ground to the canopy.

DISCUSSION

Habitat and conservation.—My field work indicates that both the Caura Antbird and the Yapacana Antbird are habitat specialists, occurring in subtypes of more widely distributed macrohabitats. *Percnostola caurensis* has been recorded over a broad elevational range, 100–1300 m (Meyer de Schauensee and Phelps 1978). In the Pantepui region this range of elevations often spans the distance between tall, seasonal humid forest and elfin cloud forest. An antbird that occurs across such a spectrum of habitats might normally be considered an ecological generalist. However, if the critical ecological factor determining its distribution is the presence of large rocks within forest regardless of elevation, then *P. caurensis* is very much a specialist. This could, in part, account for the absence of the species from so many seemingly suitable lowland sites in Bolívar and Amazonas (Campamento Junglaven: Zimmer and Hilty 1997; Brazo Casiquiare: Paynter 1982).

Percnostola caurensis may have evolved as something of a rock-specialist to occupy a

niche that is locally abundant in parts of the highly eroded Guianan Shield. Mayr and Phelps (1967:277) described the tepuis (table top mountains) of this region: "many are actually strongly dissected and strewn with isolated blocks, some more than 100 m high, and with a large variety of other rock forms." Most Caura Antbirds have been collected from the slopes of tepuis (Zimmer and Phelps 1947, Phelps and Phelps 1963, Meyer de Schauensee and Phelps 1978). The most recently collected specimen, from 1250 m at the base of Pico Maguire (edo. Amazonas, Venezuela), was from a site described as "A hanging valley in dense cloud forest with moderately tall trees, and rocky forest floor covered with thick moss" (Willard et al. 1991: 6). The apparent absence of *P. caurensis* from much of the eastern portion of the tepui region of Bolívar is a mystery.

Myrmeciza disjuncta appears to be restricted to woodlands growing on white sand soils. White sand habitats are widely but patchily distributed throughout Amazonia, with their center of distribution in the upper Río Negro region (Pires 1974, Stotz et al. 1996). White sand soils support many different types of vegetation, from scrub to tall forest (Anderson 1981). Several distinctly different types of vegetation were found growing on white sand soils in the Picua region but I found *M. disjuncta* only in the monte cerrado. Similarly, surveys of two nearby sites in Amazonas (Campamento Junglaven and Pto. Ayacucho) have failed to record *M. disjuncta* in spite of the prevalence of white sand woodlands (Zimmer and Hilty 1997). The Yapacana Antbird may therefore be restricted only to a particular type of white sand woodland, the monte cerrado. This would indicate an even patchier distribution than previously suspected and would help explain how this species has escaped detection for so long.

Both the Caura Antbird and the Yapacana Antbird appear to be locally common within their preferred habitats. The distributions of both species are centered in the lowlands or foothills of Amazonas and western Bolívar, which are among the least populated regions in Amazonia. Thus, neither species is under immediate threat of extinction. However, their patchy distributions and apparent restriction to particular microhabitats make them more vulnerable than most other birds of the Guianan lowlands. Stotz and co-workers (1996:4) have noted that ". . . the first major waves of extinctions in the Neotropics are not occurring in centers of diversity such as the Amazon. Rather, extinctions are occurring within centers of local endemism, especially among species that have evolved ecological specializations that limit their ability to adapt to human modifications of their habitats."

Before the conservation threats facing *P. caurensis* and *M. disjuncta* can be adequately assessed, we must first confirm their dependence on or preference for the microhabitats in which I found them, then attempt to quantify just how much appropriate habitat exists within their ranges. More comprehensive survey work within the region is clearly needed. Continued protection of existing parks or reserves, such as Yapacana National Park, is vital, particularly with regard to threats posed by illegal gold-mining.

Intrafamilial relationships.—The Caura Antbird was described by Hellmayr (1906) and placed in the genus *Sclateria.* The Caura Antbird was subsequently transferred to *Schistocichla* (Zimmer and Phelps 1947), which was later subsumed into *Percnostola* without elaboration by Peters (1951). Subsequent authors (e.g., Meyer de Schauensee 1966, 1970; Sibley and Monroe 1990; Monroe and Sibley 1993) have continued this treatment, recognizing five species: *P. rufifrons, P. schistacea, P. leucostigma, P. caurensis,* and *P. lophotes.* Ridgely and Tudor (1994) resurrected the genus *Schistocichla* for *schistacea, leucostigma,* and *caurensis* on the basis of their rounder, uncrested heads (crested in *P. rufifrons* and *P. lophotes*) and spotted rather than fringed wing coverts.

On purely morphological grounds, *P. caurensis, P. leucostigma,* and *P. schistacea* would appear to comprise a natural grouping. Plumage differences between *P. caurensis* and *P. leucostigma* are especially subtle; with size and soft part coloration being the most important field characters for visually distinguishing the two species (pers. obs.). Vocal similarities are less apparent, in part because of pronounced geographic variation in the vocalizations of the various named subspecies of *P. leucostigma* (pers. obs.). Indeed, some vocal differences within the *P. leucostigma* com-

plex are as great as the between species differences in the *Schistocichla* group. Given this, I feel that resolution of the intrageneric relationships of the five species currently included in *Percnostola* should await molecular comparisons, as well as a closer evaluation of vocal and morphological differences as they relate to the *P. leucostigma* group.

Almost since its description, there has been speculation regarding the placement of the Yapacana Antbird in *Myrmeciza.* Friedmann (1948:478) offered that "the species is not too distantly related to *Myrmeciza atrothorax* but is clearly specifically distinct from that form." He went on to note that Zimmer had examined the type and the paratype and had pointed out that "the general plumage has about the texture of *Cercomacra carbonaria*" (Friedmann 1948:478). Friedmann (1948) further noted Zimmer's suggestion that a fully adult male *M. disjuncta* might show a closer relationship to *Cercomacra* than was suggested by the type specimen. He also commented that "The pattern of the markings of the upperwing coverts is very like that of some forms of *Cercomacra* (*serva* for example), but the bill is that of *Myrmeciza*" (Friedmann 1948:478). Peters (1951) alluded to the seemingly polyphyletic nature of *Myrmeciza* as he defined it and made several recommendations for the placement of various species, but did not mention *M. disjuncta.* Ridgely and Tudor (1994:333) also noted the heterogeneous nature of *Myrmeciza* and suggested specifically that *M. disjuncta* may not belong in the genus and "perhaps is more closely allied to *Sclateria*". They also seemed to suggest somewhat indirectly, that *M. disjuncta* was or should be included in the formerly recognized genus *Myrmoderus.* However, I can find no evidence that *M. disjuncta* was included in the various shifts of species between *Myrmeciza* and *Myrmoderus* by Hellmayr (in Cory and Hellmayr 1924), Todd (1927), or Peters (1951).

Morphological, vocal, and behavioral characters offer contradictory clues to the possible generic affiliations of the Yapacana Antbird. *Myrmoderus* is not currently recognized, but both Todd (1927) and Peters (1951) advocated that it be reserved for [*Myrmeciza*] *loricata* and *squamosa.* The latter are clearly sibling species that share several distinctive morphological, vocal, and behavioral characters, and they are distant in all respects from *M. disjuncta* (pers. obs.). In some morphological respects, *M. disjuncta* is reminiscent of the monotypic *Sclateria,* as suggested by Ridgely and Tudor (1994), but it has fringed rather than spotted wing coverts, white tail tips, an interscapular patch, and differs greatly in both vocal and behavioral characters. The song of *M. disjuncta* is mildly reminiscent of that of various members of the *Cercomacra nigricans* group (as defined by Fitzpatrick and Willard 1990), and the plumage pattern of males, largely gray with white-fringed wingbars and white tail-tips, and females ochraceous below, fits several members of the *C. tyrannina* group. However, *Cercomacra* antbirds tend to be slender and proportionately long-tailed (Ridgely and Tudor 1994), whereas *M. disjuncta* is relatively compact and short-tailed. No *Cercomacra* approaches the white underparts of male *M. disjuncta*; the genus as a whole has gray or blackish underparts. More importantly, male-female antiphonal duets are an important component of the vocal repertoires of virtually all species of *Cercomacra* (Zimmer et al. 1997), but are not found in *M. disjuncta.*

In size, proportions, and some aspects of plumage *Myrmeciza disjuncta* is somewhat suggestive of *Hypocnemoides.* However, neither species of *Hypocnemoides* is nearly as sexually dimorphic as is *M. disjuncta,* and they lack any suggestion of the ochraceous coloration found in female *M. disjuncta. Myrmeciza disjuncta* lacks the black throat and pale eye found in *Hypocnemoides.* Vocal differences between *M. disjuncta* and *Hypocnemoides* are much greater than the morphological differences (pers. obs.). By themselves, the two species of *Hypocnemoides* form a natural grouping, with great similarities in plumage, voice, foraging behavior, and habitat use. Almost none of these characters are shared with *M. disjuncta.*

I feel that *Myrmeciza* as currently constructed is paraphyletic, with various subgroupings that do not appear to be closely allied on the basis of morphological, vocal, or behavioral characters (e.g., Peters 1951, Ridgely and Tudor 1994). None of these subgroups is a good fit for *M. disjuncta. Myrmeciza atrothorax* has been suggested as a close relative of *M. disjuncta* by Friedmann

(1948), but the males of the two species differ dramatically in plumage, and the two species share no vocal similarities that I can detect. No compelling morphological similarities clearly ally *M. disjuncta* with any other *Myrmeciza,* nor with any other antbird. Similarly, I have compared songs and calls of *M. disjuncta* to the other 18 species currently placed in *Myrmeciza* (Isler and Whitney 1999; Zimmer, unpubl. data) and can find nothing to suggest a close relationship between *M. disjuncta* and any of the other species. Relationships suggested by one or two morphological characters in one sex are contradicted by morphological characters in the other sex, vocal characters, behavioral characters, or by some combination of the three. Although past descriptions of genera have been based largely on plumage characters which may or may not have phylogenetic relevance, the addition of vocal and behavioral data adds important evidence in redefining these relationships (e.g, comments in Remsen 1997, Remsen and Schulenberg 1997). In the absence of a molecular based phylogeny the most conservative approach would be to leave *M. disjuncta* where it is, as yet another poor fit in a genus understood to be heterogeneous. However, in my opinion, the sum of morphological, vocal, and behavioral evidence would suggest that the Yapacana Antbird is monotypic, deserving of its own genus.

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HABITAT PATCH SIZE AND NESTING SUCCESS OF YELLOW-BREASTED CHATS

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ABSTRACT.—We measured vegetation at shrub patches used for nesting by Yellow-breasted Chats (*Icteria virens*) to evaluate the importance of nesting habitat patch features on nest predation, cowbird parasitism, and nest site selection. Logistic regression models indicated that nests in small patches (average diameter <5.5 m) that were parasitized by Brown-headed Cowbirds (*Molothrus ater*) experienced higher predation than unparasitized nests in large patches. Nests in large patches were more likely to become parasitized by cowbirds, as were nests with more large stems (>10 cm dbh) nearby. Patches used by chats for nesting had larger average diameters than unused patches and tended to contain more small stems. Chats appeared to prefer large patches and experienced lower nest predation there. Although they might experience higher brood parasitism frequencies in large patches, losses to parasitism were balanced by higher nesting success because the mean number of chat young that fledged did not differ between nests in small versus large patches. *Received 12 Jan. 1998, accepted 28 Dec. 1998.*

The nest "patch" has been defined as the habitat patch immediately surrounding the nest (Martin and Roper 1988). Characteristics of the songbird nesting patch may differ from the habitat available (Martin and Roper 1988; Kelly 1993; Steele 1993; Kligo et al. 1996a, b) and there may be differences between successful and unsuccessful nests according to nest patch characteristics (Martin and Roper 1988, Kelly 1993, Norment 1993, Tarvin and Smith 1995). However, there is no consensus on exactly what determines a nest patch. Petersen and Best (1985) and Martin and Roper (1988) defined the nest patch as the area within 5 m of the nest, a criterion that other studies since have adopted (Kligo et al. 1996a, b; Barber and Martin 1997). Other workers have evaluated nest patches based upon other predetermined sizes (Conner et al. 1986, Kelly 1993, Norment 1993, Tarvin and Smith 1995), multiple radius patch sizes (Petit et al. 1988, Holway 1991, With 1994), or stem density (Holway 1991, Knopf and Sedgewick 1992). Knopf and Sedgwick (1992) based their patch definition upon vegetation height and radius descriptors rather than upon pre-determined size, and concluded that individual plants probably are functionally indistinguishable to Yellow Warblers (*Dendroica petechia*), which select nests based on patch characteristics rather than the nest plant.

We examined the relationship between nest patch characteristics and nest predation, brood parasitism, and nest site selection for the Yellow-breasted Chat (*Icteria virens*). Yellow-breasted Chats are a common songbird of shrub habitats (Nolan 1963, Thompson and Nolan 1973) and at our sites often nested in conspicuous dense thickets of shrubs. We combined two approaches by measuring vegetation structure in a fixed-radius plot centered on the nest and measuring dimensions of the shrub patch in which the nest was located. Our principle questions were: (1) are chat nests in large thickets, or patches, more likely to fledge young than nests in small patches or single shrubs and trees? and (2) are chat nests that are placed further from the edge of the nesting patch more likely to fledge young? We predicted that chats nesting in larger patches at greater distances from the patch edge would be more likely to avoid predation because large patches may impede the movements of predators (Bowman and Harris 1980, Holway 1991). Additionally, we predicted that nests near greater numbers of trees would experience higher frequencies of cowbird parasitism because Brown-headed Cowbirds (*Molothrus ater*) use trees to aid in finding nests (Anderson and Storer 1976, Romig and Crawford 1995, Clotfelter 1998). We also predicted that size of nest patches would differ from the size of patches selected at random. We tested these predictions by monitoring nest success and

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cowbird parasitism of chats and by measuring vegetation at nest sites and unused sites.

METHODS

We found Yellow-breasted Chat nests at Thomas Baskett Wildlife Research and Education Center near Ashland, (Boone County) Missouri, from 1992–1994 as part of a study of shrubland birds. Study sites were six old fields ranging from 2.4 to 16.3 ha and surrounded by oak-hickory forest (see Burhans 1997 for detailed site description). We monitored nests every 3–4 days and daily toward the end of the nestling period. We considered nests that avoided predation and succeeded in fledging either chat or cowbird young as "fledged". In most cases fledged nests were identified by observing adults carrying food or scolding, or by observing fledglings. Nests that were empty on the fledging day (day 8, where day of hatching = day 0) were classified as fledged if they were active the day before. We classified nests that were empty prior to this time as depredated unless there were signs of premature fledging, such as nearby fledglings or adult feeding activity. Parasitism status was determined for all nests and only those nests that were initiated during the period of cowbird parasitism (before the second week of July) were considered in the parasitism analysis.

Vegetation samples were taken at nest sites and unused sites at the end of the nesting season. We measured nest height to the bottom of the nest cup. We also measured nest "patch", which was defined as interlocking leafy shrub or tree vegetation at nest height within which the nest plant was situated. Nest patches varied in size from the single nest tree or shrub to an entire fencerow. We measured length and width of patches to the nearest 0.1 m for distances within 3 m and paced (calibrated at 1 m/pace) to the nearest m for greater distances. "Average patch diameter" was the sum of the length of the nest vegetation clump plus the width of the clump divided by two. Nest patch diameter varied greatly among patches (median = 5.5 m, range 0.3–65 m) so we grouped nests into "large" (≥5.5 m) or "small" patches for analyses (see below). "Patch-edge distance" was the distance (to the nearest 0.1 m) from the outside rim of the nest cup to the nearest leafy edge of the nest patch. In order to further characterize patches and evaluate potential cowbird perches, we counted woody stems 11–20, 21–50, and greater than 50 cm dbh (diameter at breast-height) in an 11.3 m radius circle centered on each nest. We counted shrub and sapling stems (≥1 m high) in a 5 m radius circle around each nest in categories less than 2, 2–5, and at least 5 cm dbh. Many chat nests were placed in large blackberry (*Rubus allegheniensis*) patches in which it was difficult to count stems. For large blackberry patches (>10% of the circle) we estimated number of blackberry stems by counting the number of stems in a square meter and extrapolating to the proportion of the 5 m circle that was blackberry.

Unused sites were located by pacing in a randomly determined compass direction to the first plant encountered of the same species and size category as the nest plant (at least 40 m from the nest). As with nest sites, we took patch diameter and stem count measurements for unused patches. We did not sample vegetation for 10 nests destroyed by flooding in 1993 and storms in 1994 and did not include these nests in the analysis. We also omitted 2 nests found immediately before fledging where it was not possible to inspect chicks to determine parasitism status without forcing fledging.

Data analyses.—We evaluated fledging success using both simple nesting success (number of successful nests/total nests) and the Mayfield method (Mayfield 1961, 1975). For the Mayfield method half the number of days between subsequent visits over which a nest was empty were added to the number of previous days the nest survived to obtain the total number of observation days for a nest. When calculating daily survival probabilities we only included mortality caused by nest predation. We calculated survival probabilities and variances with standard errors according to Johnson (1979). We compared survival probabilities using CONTRAST (DOS; Sauer and Williams 1989). Another species that nested at this site (Indigo Bunting; *Passerina cyanea*) suffered higher predation at parasitized nests (Dearborn in press), so we compared daily survival probabilities between parasitized and unparasitized nests. Simple nesting success was used for logistic regression models (below). Nests that fledged at least one chick (chat or cowbird) were considered "fledged". When calculating mean number of chat young fledged, we assumed that the number successfully fledged was equal to the number of chicks last counted in the nest. We compared mean number of chat chicks fledged from nests in large versus small patches with an independent sample two-tailed *t*-test.

We analyzed both nest predation and nest parasitsm with logistic regression models. Nest height, patch distance, average patch diameter, stems defined as above, total stems 10 cm dbh or smaller ("total small stems"), and cowbird parasitism status (parasitized or not) were evaluated in the nest predation model. Frequency of parasitism has been related to nest height and nest vegetation (Hahn and Hatfield 1995, Brittingham and Temple 1996), so we similarly used logistic regression to analyze parasitism against nest height, average patch diameter, patch distance, mean stems at least 10–20, 21–50, greater than 50 cm dbh, and combined stems greater than 10 cm dbh ("total large stems"). Model building for both nest predation and parasitism models followed the method of Hosmer and Lemeshow (1989) and consisted of running univariate logistic regression models and retaining variables with *P*-values of 0.25 or less in a full model. The final reduced models included those variables with $P < 0.05$. Decisions about which variables should be left in final models were based on probability values for individual variables from a set of alternative multivariate models. We performed Hosmer and Lemeshow (1989) goodness-of-fit tests on the final models.

TABLE 1. Parameter estimates, Wald χ^2 statistics and probability levels for final nest predation (top) and nest parasitism (bottom) logistic regression models.

Model/Variable	Parameter	χ^2	*P*
Nest predation			
Parasitism	−2.23	5.44	0.02
Average patch diameter	−1.52	4.24	0.04
Nest parasitism			
Average patch diameter	2.28	5.50	0.02
Total large stems (>10 cm dbh)	0.25	5.36	0.02

Nest sites and unused sites were compared with logistic regression rather than discriminant function because of the presence of binary explanatory variables and non-normal variance of other variables (Press and Wilson 1978, James and McCullogh 1990). Nest and unused site variables were screened with univariate logistic regression models, and multivariate models were developed similarly to the predation and brood parasitism models (above). Results for statistical tests are reported as mean ± SE.

RESULTS

Nesting success and predation/parasitism models.—Daily survival estimates of Yellow-breasted Chat nests did not differ among years from 1992–1994 (1992: 0.96 ± 0.01, 1993: 0.94 ± 0.02, 1994: 0.95 ± 0.02; $\chi^2 = 0.7$, df = 2, $P > 0.05$) so data from all nests were pooled for the predation analysis (0.95 ± 0.01; $n = 48$ nests). Brood parasitism frequency was 33% ($n = 15$ nests), 36% ($n = 14$ nests) and 23% ($n = 13$ nests) for 1992, 1993, and 1994 and did not differ between years (Fisher exact test; $P > 0.05$). Cowbird parasitism averaged 31% over all years during the seasonal period of parasitism ($n = 42$ nests). Parasitized nests did not have significantly different survival rates than unparasitized nests (parasitized nests 0.94 ± 0.02; unparasitized nests 0.96 ± 0.01; $\chi^2 = 1.7$, df = 1, $P > 0.05$).

Nest predation was best explained by a final logistic regression model including parasitism status and average patch diameter (Table 1; Log likelihood for model = 51.8, $\chi^2 = 8.7$, df = 2, $P = 0.01$). Nests that were parasitized and in small patches were more likely to suffer predation. However, the nest parasitism model indicated that nests in large patches were more likely to become parasitized. The nest parasitism model included the variables average patch diameter and total large stems (Table 1; Log likelihood for model = 40.9, $\chi^2 = 11.1$, df = 2, $P = 0.004$). Nests with more large stems were more likely to be parasitized, but large patches did not have greater mean values for total large stems than did small patches (large patches 2.27 ± 0.67; small patches 3.45 ± 1.01; $t = 0.99$, df = 40, $P > 0.05$). Distance from the nest to the edge of the patch tended to be greater for parasitized nests (Table 2), but was eliminated from the parasitism models because of the higher probability values associated with average patch diameter, with which patch-edge distance was positively correlated prior to transformation of the former variable ($r = 0.39$, $P = 0.009$). Mean number of chat young fledged did not vary between nests in small versus large patches (small patches: 1.04 ± 0.34 chat young per nest; large patches 1.43 ± 0.36 chat young per nest; $t = -0.79$, df = 44, $P > 0.05$).

Nest sites versus unused sites.—Univariate logistic regression models indicated that nest sites were situated in larger patches than unused sites (Table 3). When variables were combined in the multivariate model only average patch diameter was significant (Log likelihood for model = 121.07, $\chi^2 = 12.0$, $P = 0.001$).

DISCUSSION

As predicted, logistic regression models indicated that Yellow-breasted Chats experienced less predation in larger nest patches. As with Indigo Buntings at these sites (Dearborn, in press), predation was related to parasitism status at Yellow-breasted Chat nests; nests that were parasitized were more likely to experience predation. Chats tended to place nests in larger patches with more small stems than those in unused sites. Nests that were placed farther from the patch edge were more sus-

TABLE 2. Means (± standard error), parameter estimates, Wald χ^2 statistics, and probability levels for individual variables from logistic regressions on predation and parasitism.

Variable	Predation					Parasitism				
	Depredated	Fledged	Parameter	χ^2	P	Parasitized	Unparasitized	Parameter	χ^2	P
Parasitism (% of nests)	37%	11%	−1.55	3.33	0.07	—	—	—	—	—
Average patch diameter (% nests in large patches)	43%	63%	−0.83	1.84	0.18	77%	41%	1.55	4.19	0.04
Patch-edge distance (m)	0.78 ± 0.15	1.22 ± 0.42	−0.31	0.98	0.32	1.21 ± 0.30	0.70 ± 0.09	0.97	3.47	0.06
Nest height (m)	0.69 ± 0.06	0.74 ± 0.07	−0.52	0.29	0.59	0.70 ± 0.05	0.67 ± 0.07	0.37	0.10	0.75
Stems <2 cm dbh	347.04 ± 141.67	276.74 ± 181.35	0.00	0.1	0.75	—	—	—	—	—
Stems 2–5 cm dbh	3.00 ± 0.59	7.68 ± 2.26	−0.15	3.55	0.06	—	—	—	—	—
Stems 5–10 cm dbh	1.39 ± 0.31	1.68 ± 0.58	−0.07	0.24	0.62	—	—	—	—	—
Total small stems (≤10 cm dbh)	351.43 ± 141.43	286.11 ± 180.84	0.00	0.09	0.77	—	—	—	—	—
Stems 11–20 cm dbh	—	—	—	—	—	2.31 ± 0.71	1.38 ± 0.38	0.18	1.52	0.22
Stems 21–50 cm dbh	—	—	—	—	—	2.08 ± 0.78	0.69 ± 0.29	0.31	3.52	0.06
Stems >50 cm dbh	—	—	—	—	—	1.54 ± 1.04	0.00 ± 0.00	13.53	0.00	0.97
Total large stems (>10 cm dbh)	—	—	—	—	—	4.54 ± 1.38	2.07 ± 0.57	0.16	3.35	0.07

ceptible to parasitism (Table 2); however, we were unable to separate the importance of patch-edge distance from the size of the patch itself (patch diameter). Although nests in large patches were more likely to become parasitized, higher nesting success in large patches compensated for decrements in fitness caused cowbird parasitism because the number of host young that fledged was equal between small and large patches.

Petersen and Best (1985), Knopf and Sedgwick (1992), and Holway (1991) found that birds selected large shrubs or shrub stands for nest placement. Holway (1991) and Knopf and Sedgwick (1992) suggested that large patches offer improved nest concealment; Holway (1991) also believed that large patches could impede the movements of mammals, and could contain more potential nest sites for predators to search (see also Martin and Roper 1988).

Several researchers have found that birds place nests in denser cover than in unused sites (Knopf and Sedwick 1992, Sedgwick and Knopf 1992). Holway (1991) and Steele (1993) found higher foliage and shrub density at nests of Black-throated Blue Warblers (*Dendroica caerulescens*) than at random points. Wray and Whitmore (1979) and Norment (1993) found that successful Vesper Sparrow (*Pooecetes gramineus*) and Harris Sparrow (*Zonotrichia querula*) nests tended to be placed in denser cover than unsuccessful nests.

Chat nests parasitized by Brown-headed Cowbirds were more likely to become depredated. Dearborn (in press) found higher daily mortality at parasitized nests of Indigo Buntings in a five year study from the same sites we used. He suggested that louder vocalization by cowbird nestlings was partly the cause, although daily mortality was also higher at parasitized bunting nests during the incubation stage. In our study, the sample size of parasitized nests with cowbird chicks was too small ($n = 4$) to adequately compare daily mortality between nests with cowbird chicks and those without (Hensler and Nichols 1981).

Parasitized nests had more potential cowbird perches (large stems) than unparasitized nests. Recent studies have documented the importance of perch proximity in brood parasitism in both cuckoos (*Cuculus canorus*; Al-

TABLE 3. Means (± standard error), parameter estimates, Wald χ^2 statistics, and probability levels for individual variables from univariate logistic regressions comparing nest sites and unused sites.

Variable	Nest sites	Unused sites	Parameter	χ^2	*P*
Average patch diameter (% in large patches)	52%	19%	1.55	10.91	0.001
Stems <2 cm dbh	313.23 ± 108.47	60.19 ± 11.49	0.00	2.47	0.12
Stems 2–5 cm dbh	5.44 ± 1.14	4.17 ± 1.01	0.02	0.68	0.41
Stems 5–10 cm dbh	1.48 ± 0.29	1.10 ± 0.24	0.11	0.99	0.32
Stems 11–20 cm dbh	1.58 ± 0.31	2.15 ± 0.42	−0.09	1.12	0.29
Stems 21–50 cm dbh	1.06 ± 0.29	1.21 ± 0.32	−0.03	0.12	0.73
Stems >50 cm dbh	0.04 ± 0.03	0.02 ± 0.02	0.71	0.33	0.57
Total small stems (≤10 cm dbh)	320.14 ± 108.19	65.45 ± 11.51	0.00	2.77	0.10
Total large stems (>10 cm dbh)	2.69 ± 0.54	3.38 ± 0.65	−0.04	0.66	0.42

varez 1993, Øien et al. 1996) and cowbirds (Romig and Crawford 1995, Clotfelter 1998; see also Anderson and Storer 1979). Previous studies (Burhans 1997) on Field Sparrows (*Spizella pusilla*) and Indigo Buntings nesting at Thomas Baskett Wildlife Research and Education Center indicated no direct relationship between perches near the nest and frequency of parasitism. However, Yellow-breasted Chat nest sites generally are situated in patches with more trees and shrubs than old field nests of Indigo Buntings and Field Sparrows. The higher frequency of parasitism in large patches was not an artifact of patch size, because large patches did not necessarily contain more total large stems.

Nest site selection, nesting success, and frequency of cowbird parasitism at Yellow-breasted Chat nests appear to be influenced by patch size. However, relaxed predation in large patches did not improve host fledging success, because chats were more likely to become parasitized in large patches and fledge fewer of their own young. Although predation and parasitism appeared to differ across patch sizes, the effects of patch size on host fitness appear to cancel each other out. Future studies should look further at interactions between site selection, brood parasitism, and predation, and investigate tradeoffs in reproductive success associated with these factors according to different types of nest sites.

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AVIFAUNA OF A PARAGUAYAN CERRADO LOCALITY: PARQUE NACIONAL SERRANÍA SAN LUIS, DEPTO. CONCEPCIÓN

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ABSTRACT.—We recorded 181 avian species at the Paraguayan Cerrado site, Parque Nacional Serranía San Luis, depto. Concepción, including the first record of Veery (*Catharus fuscescens*) for the country. We obtained further evidence of hybridization between White-bellied (*Basileuterus hypoleucus*) and Golden-crowned (*B. culicivorus*) warblers. Our results combined with those of earlier workers document a total of 219 species for this area. Pronounced differences in species composition exist between San Luis and a nearby Cerrado locality. Three threatened and four near-threatened species were recorded at San Luis. Since our inventory the area that we worked was traded for an adjacent, less human impacted sector of similar size. The new park boundary contains relatively pristine campo (grassland), which is an important habitat for a number of resident and migrant species suspected to be suffering serious population declines. *Received 29 Jan. 1998, accepted 14 Nov. 1998.*

RESUMEN.—Se registraron 181 especies de aves en el Parque Nacional Serranía San Luis, en el cerrado del Paraguay, depto. Concepción. La lista incluye el primer registro de *Catharus fuscescens* para el país, y más evidencia de hibridización entre los parúlidos *Basileuterus hypoleucus* y *B. culiciviorus*. En combinación con los resultados de investigadores anteriores, han sido registrado 219 especies de aves para la zona. Existen diferencias marcadas en la composición avifaunística entre San Luis y otra localidad cercana en cerrado. Se registraron tres especies amenazadas y cuatro casi-amenazadas en la zona. Desde que se hizo el presente estudio, se cambió. el área de estudio por otro adyacente, menos impactado y de extenso similar; esta zona abarca más del campo (pastizal) en buen estado de conservación, el cual es un refugio para varias especies residentes y migratorias que se cuentran en declives poblacionales.

The Cerrado is the second largest ecological region in South America (Ab'Saber 1977), but has only recently attracted the attention of avian biogeographers (Haffer 1985; Silva 1995a, b, c). Silva (1995a) demonstrated that about 70% of the Cerrado is inadequately sampled and that the southern component especially is poorly known and most heavily impacted by human activities. The Cerrado reaches its southern terminus in northeastern Paraguay, where it interdigitates with two other physiogeographic and biotic regions: the Chaco and the Atlantic Forest (Hayes 1995a). The lack of a quantitative inventory of this region, coupled with the potential for extensive biotic interchange among the contiguous regions, make the Paraguayan Cerrado important for its unique contribution to the biodiversity of the Cerrado. In this paper, we present a preliminary avifaunal inventory for the 10,273 ha Parque Nacional Serranía San Luis, created in 1991 to preserve a representative sample of the Paraguayan Cerrado (Dirección de Parques Nacionales y Vida Silvestre 1993). We have incorporated results from earlier work in the region to provide a more comprehensive list for this area. The San Luis list is compared to another well-surveyed Paraguayan Cerrado locality to examine avian species turnover. Selected species accounts are provided where additional comment is merited to clarify status, distribution, migration, food habits, hybridization, and plumage characters.

STUDY AREA AND METHODS

We worked at the southern end of Parque Nacional Serranía San Luis (22° 40′ S, 57° 21′ W; taken with Global Positioning System at park headquarters; Fig. 1) from 19–31 October 1996, and RCF revisited the site from 29 November to 7 December 1996. The park is located in the Serranía San Luis, an isolated, low-lying (max. elevation 500 m) set of limestone hills mostly covered with semihumid forest. Approximately 5,300 ha is cultivated grassland with about 70% of this habitat now occupied by the aggressive African grass *Hyparrhenia rufa* (Poaceae). The dominant savannah tree, *Tabebuia aurea* (Bignoniaceae), was often associated with *Astronium urundeuva* (Anacardiaceae), *Anadenanthera colubrina* (Leguminosae), and *Rhamnidium elasocarpum* (Rhamnaceae; Consorcio Parelc-Foragro-Porto Real, unpubl. report). Hillsides were

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FIG. 1. Locations of Parque Nacional Serranía San Luis and Parque Nacional Cerro Corá.

covered with shallow, rocky soil, resulting in shorter, xeric forest; the more level areas along two arroyos bordering the western and eastern sides of the park held taller, more humid forest. Terrestrial bromeliads and cacti were common in the dense, thorn-covered understory on slopes and on isolated woodland in the campo (open grassland). The largest area of campo, about 4 × 2 km, had a few woodlots, some only a few meters square. The upland forest and isolated woodlands had uneven canopies and were relatively short, with few trees exceeding 20 m. Prominent trees included: *Amburana cearensis* (Leguminosae), *Aspidosperma pyrifolium* (Apocynaceae), *Calycophyllum multiflorum* (Rubiaceae), and *Astronium urundeuva* (Anacardiaceae). The understory was dominated by trees of the genus *Trichilia* (Meliaceae).

Forests along the arroyos, especially east of Tagatlya Guazu arroyo at the headquarters, were taller and more humid, with some trees exceeding 40 m. These forests were heavily disturbed by selective logging, and treefall gaps with dense understory were common. Vine tangles were also more common than in the upland forest, especially about 2 km east of the park headquarters. Tall arborescent bamboo (*Guadua* spp.) was primarily restricted to disturbed areas along the arroyos.

This area is very seasonal with a cool, dry climate from April through most of September when temperatures occasionally drop to near 0° C. Temperature and rainfall increase in October and November with December through March being relatively hot and humid. Average annual rainfall is 1300 mm with considerable variation (A. Acosta, pers. comm.), and average annual temperature is 24° C (Consorcio Parelc-Foragro-Porto Real, unpubl. report). During our stay, weather was highly variable. On the evening of 19 October a major storm system from the southeast brought heavy rains (70 mm) and strong winds. Precipitation also occurred on 25 October, 12 mm; 26 October, 2 mm; and 27 October, 6 mm. Apparently it did not rain between our October and December surveys (A. Acosta, pers. comm.); however, it rained five of nine days during the latter inventory period. Temperature highs ranged from 24–38° C. The low was 18° C at dawn on 23 October. We did not record the temperature during November and December.

Four mist-nets were opened on the afternoon of 19 October, and 6 on 20 October; 15 nets were maintained from 21–30 October, for a total of about 11,400 mist-net-hr. All mist-nets were positioned in mesic forest bordering Tagatlya Guazu arroyo; the most distant nets were about 1.5 km east of the headquarters. Most nets were moved every three to four days. Nets were typically opened at dawn and closed about noon, rarely at sunset. Our inventory was confined to about 4 km of forest trail east of the headquarters, about 5 km of dirt road to the north of the headquarters, and about 2 km of dirt road from the headquarters to the southwest entrance. On most mornings, RCF and NHR worked the nets and adjacent forest, while MBR made independent surveys of other areas from predawn until 11:00 or 12:00. Occasional forays were made in the afternoon. Nocturnal fieldwork was limited to nights with a full moon in October.

Specimens were deposited at the University of Kansas Natural History Museum (KU), Lawrence, Kansas and Museo Nacional de Historia Natural del Paraguay (MNHNP), Asunción, Paraguay. Tissue samples were taken from every nonfluid preserved specimen and deposited at KU. Tape recordings will be deposited at the Library of Natural Sounds, Cornell University, Ithaca, New York.

To provide a more complete inventory of the Serranía de San Luis region, we have integrated our species list (Appendix) with results from earlier work in San Luis de La Sierra that was conducted in September–October 1931 by Hans Krieg (referred to as "Apa-Bergland"; summarized in Laubmann 1939, 1940). Results from Kreig's expeditions to Zanja Morotí, Centurión, and Estrella, Concepción were not included because these areas are farther removed from San Luis, and the Estrella site was at the Río Apa. We presume that the riparian habitat and associated fauna along the Río Apa is somewhat distinct from that at San Luis. We also excluded specimens taken by Emil Kaempfer at La Fonciere, Concepción (deposited at American Museum of Natural History; Floyd Hayes and Paul Sweet, pers. comm.). Except where noted otherwise, we follow Hayes (1995a) for taxonomy and nomenclature.

RESULTS

We recorded a total of 181 species (Appendix), of which three are designated as threatened and four as near-threatened (Collar et al. 1992, 1994). Three of the 29 species identified by Silva (1995c) as endemic to the Cerrado, Planalto Foliage-gleaner (*Philydor dimidiatus*), Curl-crested Jay (*Cyanocorax cristatellus*), and Black-throated Saltator (*Saltator*

atricollis), have been recorded at San Luis. We recorded four species that Silva (1995c) did not list for the Cerrado: South American Painted-Snipe (*Rostratula semicollaris*), White-naped Xenopsaris (*Xenopsaris albinucha*), Red-crested Cardinal (*Paroaria coronata*), and Golden-winged Cacique (*Cacicus chrysopterus*). Hayes (1995a) did not list *R. semicollaris, X. albinucha,* Golden-green Woodpecker (*Piculus chrysochloros*), nor Dark-throated Seedeater (*Sporophila ruficollis*) as occurring in his "Campos Cerrados" category.

At least 64 of the 92 species we collected had enlarged gonads indicating reproduction, and nests or recently fledged young were observed for 12 additional species that were not collected (Appendix). Based on vocal activity and behavior, breeding was suspected for several species not collected, such as Bare-faced Currasow (*Crax fasciolata*), Red-legged Seriema (*Cariama cristata*), Short-tailed Nighthawk (*Lurocalis semitorquatus*), and Crowned Slaty Flycatcher (*Griseotyrannus aurantioatrocristatus*). Hence, at least 80 species were actively nesting at the time of our studies (mid-October–early December). One Nearctic, one intratropical, and at least 32 Austral migrants were recorded (Appendix; migrant terminology follows Hayes 1995b).

Nocturnal avian vocal activity was most pronounced shortly after dusk and in the hour before dawn, with the greatest activity on nights with the brightest moon light. The Ferruginous Pymy-Owl (*Glaucidium brasilianum*) and both screech-owls (*Otus*) were heard nightly, as were Pauraque (*Nyctidromus albicollis*), Rufous Nightjar (*Caprimulgus rufus*), and Common Potoo (*Nyctibius griseus*). The Little Nightjar (*C. parvulus*) was never heard, even though individuals and a nest with an egg and a day-old young, were collected at the edge of camp.

Rodent eating hawks and owls were not well represented in the San Luis avifauna. A possible causal explanation is that rodent diversity and density were low. During October, we observed no evidence of rodents. Squirrels are unknown from this part of Paraguay; during seven nights in late November–early December Texas Tech University mammalogists captured few mammals in a variety of habitats (M. Gorresen, pers. comm.). Raptor species expected, but not detected include: Great Black Hawk (*Buteogallus urubitinga*), Harris's Hawk (*Parabuteo unicinctus*), all *Buteo* species, Spectacled Owl (*Pulsatrix perspicillata*), Great Horned Owl (*Bubo virginianus*), and *Asio* spp. Only the Savannah Hawk (*Buteogallus meridionalis*) and Ornate Hawk-Eagle (*Spizaetus ornatus*) were recorded (both rarely) among the species of raptor whose diets include a relatively high percent (>25%) of rodents (Brown and Amadon 1968, del Hoyo et al. 1994).

SPECIES ACCOUNTS

Snail Kite (Rostrhamus sociabilis).—On 22 and 23 October, we observed two flocks of 154 and 33 individuals (mostly adults), respectively, pass through the campo. The birds appeared from the north and landed on the ground, in bushes, and in isolated palm trees, flying only a few meters between each perch. When the groups came to the forested Tagatlya Guazu arroyo at the south end of the park, they rose as a group into the air and disappeared to the south. Snail Kites were not observed during late November–early December. Our observations coincide with prior observations of migratory movements of this species in Paraguay (Hayes et al. 1994).

Crowned Solitary Eagle (Harpyhaliaetus coronatus).—An adult with a tegu lizard (Teiidae; *Tupinambis* sp.) in its talons was flushed from a large tree at the forest/campo edge on 19 October. It landed in the top of a nearby tree where it sat for about 3 min before it disappeared with the lizard in its talons. This species is considered vulnerable ("taxa believed likely to move into the endangered category in the near future if the causal factors continue operating"; Collar et al. 1992) and has been recorded few times from Paraguay with only one prior record for depto. Concepción (Hayes 1995a). Very little is known about this eagle's prey (Collar et al. 1992), and our observation is apparently the first of it taking a tegu. It is known to take small mammals (Collar et al. 1992, del Hoyo et al. 1994), but we saw no signs of rodents. Del Hoyo and coworkers (1994) noted that this eagle has short toes characteristic of snake eaters.

Bare-faced Curassow (Crax fasciolata).—Given that cracids are usually one of the first avian species to disappear because of exces-

sive hunting, we were encouraged to find at least seven territorial males calling along about 4 km of trail on the east side of Tagatlya Guazu arroyo. Males called daily in October from predawn until about 07:00, occasionally until 10:00. We did not hear males in the drier forest; however, we surveyed only a relatively small area of this forest type at the optimal time of day. No calling was heard in late November–early December.

Reddish-bellied Parrot (Pyrrhura frontalis).—This species was common in both forest types. Birds collected (KU 88346, MNHNP) at San Luis were typical of the race *P. f. chiripepe,* and showed no sign of hybridization with *P. devillei* as has been reported in areas just northwest of San Luis (Short 1975).

Rufous Nightjar (Caprimulgus rufus).—The single male (testes 11 × 6 mm; KU 88350) obtained was not assignable to either the nominate race or to southern *C. r. rutilus.* Like birds from central Brazil (Goias, Bahia; Robbins and Parker 1997), the San Luis specimen's wing and tail measurements (173.6 and 119.7 mm, respectively) fall within the range of variation of the nominate race, but plumage color and pattern are closest to *C. r. rutilus.*

Blue-crowned Motmot (Momotus momota).—Our specimens (KU 88580, MNHNP) from San Luis represent only the fifth locality in Paraguay (Hayes 1995a, Ericson and Amarilla 1997), and the first for depto. Concepcíon. Both specimens, a probable pair, lack the bluish-green throat of eastern Bolivian and Argentinian *M. m. pilcomajensis;* the greenish underparts were washed with cinnamon, especially on the abdomen, which is more typical of southern Brazilian *M. m. simplex.* Chapman (1923) was uncertain in assigning a specimen from western São Paulo to either of the above races and concluded that there was considerable variability in this species south of the Amazon. Ericson and Amarilla (1997) believed that specimens they obtained from Parque Nacional Defensores del Chaco, depto. Chaco were intergrades between the above forms.

Planalto Foliage-gleaner (Philydor dimidiatus).—Known in most of the literature as the Russet-mantled Foliage-gleaner, we follow Ridgely's and Tudor's (1994) appropriate suggestion for an English name. Two pairs of this poorly known foliage-gleaner were encountered about 2 km east of the headquarters (KU 88362, 88363, MNHNP). Both pairs were observed foraging 2–4 m above the ground in relatively dense understory. One pair was associated with a understory mixed-species flock. Ridgely's and Tudor's (1994) description of the song and call accurately describe what we recorded, with the San Luis birds sounding very similar to birds from Patios de Minas, Minas Gerais (tape recording by Andrew Whittaker). Plumage differentiation and taxonomy of this species will be presented elsewhere.

Bare-throated Bellbird (Procnias nudicollis).—San Luis lies at the western limit of this species' range (Snow 1982, Hayes 1995a). In October, two birds were recorded. An adult male (KU 88873) sang for more than 15 min during mid-morning on 24 October from a leafless, uppermost branch of one of the tallest trees (ca 40 m) in the mesic forest east of the headquarters. Only one or two other individuals were heard in October, both gave the *bock* call a few times, on two separate occasions. In November and December, RCF heard at least 12 displaying males daily along about 4 km of trail east of Tagatlya Guazu arroyo. An immature male (KU 88387: testes 8 × 4 mm) was one year old based on plumage (Snow 1973) and bursa size (8 × 8 mm). The plumage of this specimen resembles closely that of an adult female (Snow 1982, Sick 1993), except that the head is entirely black and the abdomen and crissum are primarily white instead of pale yellow. It was in moderate to heavy body molt, with #5 primary in molt (primaries 1–4 fresh). Secondary 7 or 8 (one is missing on each side) was in molt. Secondary 9 was very worn, and the others appeared lightly worn. The central pair of rectrices was in molt with all other rectrices heavily worn.

This bellbird has been documented as migratory in the southeastern part of its Brazilian range (Belton 1985, Sick 1993); in Misiones, Argentina it is apparently only transient (M. Barnett in Lowen et al. 1996b). In Paraguay it is thought to occur year round in depto. Canendiyú and probably depto. Amambay (Madroño and Esquivel 1995). Its status elsewhere in Paraguay is unclear (Lowen et al. 1996b). Our limited fieldwork at San Luis suggests it may occur there only seasonally. If this bell-

bird covers great distances in its seasonal movements, then it may be especially vulnerable to habitat fragmentation. Willis (1979) regarded large canopy frugivores to be vulnerable because of their reliance on spatially and temporally patchy resources. This bellbird and the Red-ruffed Fruit Crow (*Pyroderus scutatus*) completely disappeared from forests that had been fragmented (largest fragment 198 ha) in the Lagoa Santa area of Brazil (Christiansen and Pitter 1997).

Veery (Catharus fuscescens).—We netted an immature male (KU 88484) on 30 October. This record is the first for Paraguay, and represents one of the southernmost records for the continent (McFarlane 1974; Remsen and Traylor 1983; Ridgely and Tudor 1989; Willis and Oniki 1993; D. Stotz, pers. comm.). The specimen is referable to the nominate subspecies. All three Bolivian specimens originally identified as *C. f. salicicola* by Remsen and Traylor (1983) are now thought to be of either the nominate race or *C. f. fuliginosa* (V. Remsen, D. Stotz, pers. comm.). No subspecific determinations have been made for southeastern Brazilian specimens.

White-bellied Warbler (Basileuterus hypoleucus).—The presence of yellow in the lower underparts of a few specimens from several areas and observation of mixed-species pairs document the occasional hybridization between *B. hypoleucus* and the Golden-crowned Warbler (*B. culicivorus*; Hellmayr 1935, Willis 1986, Remsen and Traylor 1989, Silva 1991), although this literature has been overlooked in recent paruline summations (Ridgely and Tudor 1989, Curson et al. 1994). All four specimens prepared as skins from San Luis show signs of hybridization with varying amounts of pale yellow on the center of the abdomen and lower flanks (compared with color plate and descriptions in Silva 1991). We agree with prior assessments that this color is indicative of gene flow between *B. hypoleucus* and *B. culicivorus,* and not with *B. flaveolus* as implied in Hayes (1995a) for the following reasons. Contrary to S. LaBar (in Hayes 1995a), the vocalizations of *B. hypoleucus* are not more similar to those of *B. flaveolus* than to those of *B. culicivorus.* In fact, the vocalizations of *B. hypoleucus* and *B. culicivorus* are so similar that both species respond to play-back recordings of each other's song (Silva 1991). Neither of these taxa's song resembles those of *B. flaveolus,* whose vocalizations and behavior clearly align it with the *Phaeothlypis* assemblage (Ridgely and Tudor 1989; MBR, pers. obs.). Furthermore, the plumages and behaviors of *B. hypoleucus* and *B. culicivorus* are very similar (Silva 1991; MBR, pers. obs.), unlike the phaeothlypine-like *B. flaveolus.* We originally interpreted Hayes' (1995a) statement of "a mixed family of *B. hypoleucus* and *B. flaveolus* (two of each) at Estancia Fonciere [depto. Concepción]" as meaning mixed-species pairs; his intent, however, was to report "two of each species intermingling together" (F. E. Hayes, pers. comm.). Willis (1986) observed only a single mixed pair of *B. hypoleucus* and *B. culicivorus*; all other pairs were conspecific. Nevertheless, Silva (1991) documented more extensive hybridization in southeastern Brazil and treated the two species as conspecific. To our knowledge, all apparent hybrid morphotypes are *B. hypoleucus*-like, i.e., ventrally yellow *B. culicivorus*-like birds with some white are unknown. Presumably the situation in Paraguay is similar to that in Brazil (Willis 1986, Silva 1991), with hybridization apparently occurring only at ecotones where the dry forest inhabiting *B. hypoleucus* meets the moist forest inhabiting *B. culicivorus.* Typical *B. culicivorus* have been collected at Parque Nacional Cerro Corá, depto. Amambay, only about 130 km east of San Luis (Fig. 1), where patches of moist forest are present (MNHNP specimens, Hayes and Scharf 1995).

Screaming Cowbird (Molothrus rufoaxillaris).—Throughout most of its range, this brood parasite has been documented to specialize on Bay-winged Cowbirds (*Molothrus badius*; Friedmann 1963, Fraga 1986); however, Sick (1993) and Fraga (1996) demonstrated that *M. rufoaxillaris* parasitizes the Chopi Blackbird (*Gnorimopsar chopi*) in the absence of *M. badius.* Our limited observations at San Luis also suggest that *M. rufoaxillaris* is parasiting a host other than *M. badius.* Male *M. rufoaxillaris* and Shining Cowbirds (*Molothrus bonariensis*) were observed displaying within 15 m of each other to blackish-appearing female cowbirds in areas where the open forest and campo interdigitated. Given that no *M. badius* were observed at San Luis, we presume that *M. rufoaxillaris* was

parasitizing *Gnorimopsar chopi,* which was fairly common in the area. Unless male *M. rufoaxillaris* and *M. bonariensis* are vocalizing, they are extremely difficult to distinguish under field conditions (Ridgely and Tudor 1989). However, Ridgely and Tudor (1989) stated that pronounced plumage differences in females (grayish-brown in *M. bonariensis*; blackish in *M. rufoaxillaris*) could aid in identification in areas of sympatry. Our work at San Luis, coupled with museum and literature reviews, demonstrates that an unknown proportion of female *M. bonariensis* in southern South America also have blackish plumage. Two adult female *M. bonariensis* collected at San Luis (KU 88485, MNHNP; others observed) were glossy, bluish-black on all but the lower ventral surface and tail. Under field conditions, these females closely resembled accompanying males; only under excellent light conditions were plumage differences detected. This male-like plumage in female *M. bonariensis* is not limited to Paraguay, as bluish-black females that are very similar to the San Luis birds have also been collected from southeastern Brazil and extreme northeastern Argentina (Friedmann 1927, Sick 1993; KU 65019). Observers should exercise caution in identifying these cowbirds in areas of sympatry based on female plumage patterns. Data are needed on what proportion of nominate female *M. bonariensis* have male-like plumage.

DISCUSSION

Silva (1995a) used two criteria—a minimum of 100 species recorded and at least 80 specimens collected—for defining a Cerrado locality as minimally sampled. Based on his criteria, our results (181 species, 220 specimens) would be classified as a relatively thorough Cerrado inventory; however, our results are clearly preliminary. The inclusion of Krieg's results (Laubmann 1939, 1940) puts the Serranía de la San Luis species list at 219. With additional work, we predict that the Parque Nacional Serranía San Luis avifauna will surpass 250 species. Surveys are needed at the drier northern end of the park, where such species as Rusty-backed Antwren (*Formicivora rufa*) and Rufous-sided Pygmy-Tyrant (*Euscarthmus rufomarginatus*) may occur. From our limited observations, it is clear that San Luis is an important site for grassland and forest Austral migrants, and we predict that the majority of the species to be added to the San Luis list will be from this component. Year round surveys are needed to clarify the status of many species.

Although San Luis is one of the Cerrado sites closest to the Chaco, only one species primarily restricted to the Chaco was found there: the Great Rufous Woodcreeper (*Xiphocolaptes major*). Considerable plumage variation in the two specimens collected of this species obfuscates subspecific determination. For the Olivaceous Woodcreeper (*Sittasomus griseicapillus*), the nominate form, principally of the Chaco, was present; for the Narrow-billed Woodcreeper (*Lepidocolaptes angustirostris*) specimens collected were assignable to the ventrally heavily streaked nominate form than to the ventrally unmarked Cerrado form, *L. a. bivittatus.*

The Atlantic Forest avifauna is also poorly represented at San Luis, with only six species recorded: Reddish-bellied Parakeet (*Pyrrhura frontalis*), Variable Screech-Owl (*Otus atricapillus*), Rufous-capped Motmot (*Baryphthengus ruficapillus*), Ochre-breasted Foliage-gleaner (*Philydor lichtensteini*), Eared Pygmy-Tyrant (*Myiornis auricularis*), and the Bare-throated Bellbird. The minimal Atlantic Forest avifaunal contribution to San Luis contrasts with that of the only other Paraguyan Cerrado site that has been adequately inventoried. A total of 201 species have been recorded at nearby Parque Nacional Cerro Corá (Hayes and Scharf 1995; R. Clay, pers. comm.). Twenty-five Atlantic Forest species, including all six known from San Luis, have been reported from Cerro Corá. Eliminating water inhabiting species (herons, waterfowl, migratory shorebirds, kingfishers, marsh dwelling passerines), 61 Cerro Corá species have not been recorded at San Luis, whereas 62 species have been recorded at San Luis and not Cerro Corá. Additional surveys at both sites undoubtedly will reduce the uniqueness of each site; nevertheless, the presence of humid forest patches at Cerro Corá and campo at San Luis explain genuine species differences between these sites. The humid forest element at Cerro Corá is composed not only of species primarily restricted to Atlantic Forest, but also of species more widely distributed in

humid forest across much of South America, such as Plain Antvireo (*Dysithamnus mentalis*) and Red-rumped Cacique (*Cacicus haemorrhous*). Moreover, the difference in the number of hummingbird species between the two areas is striking, with ten species [Rufous-throated Sapphire (*Hylocharis sapphirina*) being added since Hayes and Scharf 1995; R. Clay, pers. comm.] known from Cerro Corá, but only two from San Luis. The pronounced avifaunal differences between these nearby localities support Silva's (1995c) assertion that additional Cerrado inventories are needed.

Only 3 of the 29 Cerrado endemic species (Silva 1995c) have been found at San Luis. We predict that additional work in the area will document at least 6 more Cerrado endemics: White-winged Nightjar (*Caprimulgus candicans*), White-lored Spinetail (*Synallaxis albilora*), Chestnut-capped Foliage-gleaner (*Hylocryptus rectirostris*), Collared Crescentchest (*Melanopareia torquata*), Reiser's Tyrannulet (*Phyllomyias reiseri*), and Helmeted Manakin (*Antilophia galeata*), which have been found at other Paraguayan Cerrado sites (Laubmann 1939, 1940; Hayes 1995a; Lowen et al. 1996a). Hence, maximum Cerrado endemic species diversity at San Luis is expected to be about nine species. Many of the remaining Cerrado endemic species have restricted geographic ranges; six have extremely small distributions (Silva 1995c). Indeed, one generalization that can be made of the Cerrado endemics is that most are not widespread in the region. Even in the Cerrado's geographic center (eastern Mato Grosso/west-central Goias), only about two-thirds of the endemics have been found. Several factors may contribute to the somewhat reduced species diversity in Paraguay, (1) less than an estimated 5% of the total Cerrado habitat is found in Paraguay; (2) northern Paraguay is at the southern limit of this habitat's current distribution; and (3) Paraguay has not had the geographic isolating mechanisms that have promoted speciation in other parts of the Cerrado. However, comparable numbers of endemics to Paraguay are found in other peripheral Cerrado areas, such as western Mato Grosso and northern Goias; hence, the Paraguayan Cerrado is not especially depauperate when compared across the range of the habitat.

The importance of Parque Nacional San Luis cannot be overly stressed. Since our inventory the area that we inventoried was traded for an adjacent, less human impacted sector, formerly known as Estancia Garay Kue (R. Clay and A. Madroño, pers. comm.). The new park boundary apparently encloses about 4500 ha of relatively pristine grassland. This takes on special conservation significance given that virtually all grassland habitat in Paraguay has been moderately impacted by humans (Clay et al. 1998). Indeed, grasslands are one of the most threatened habitats on the continent (Goriup 1988, Bates et al. 1992, Stotz et al. 1996, Silva et al. 1997). The grasslands at San Luis are critical to several avian species, both resident and migrant. Three of the near-threatened avian species are grassland-inhabiting: Greater Rhea (*Rhea americana*), Cock-tailed Tyrant (*Alectrurus tricolor*), and Dark-throated Seedeater (*Sporophila ruficollis*). Moreover, we suspect that the poorly-known and critically endangered White-winged Nightjar (*Caprimulgus candicans*) occurs in the San Luis area. This spectacular nightjar was only recently documented in Paraguay (Lowen et al. 1996a), and quite surprisingly, in eastern Bolivia (Davis and Flores 1994). Prior to these recent records it was known only from a few sites in central Brazil (Collar et al. 1992). Further surveys of this pristine grassland may yield additional grassland specialists, e.g., Bearded Tachuri (*Polystictus pectoralis*) and Sharp-tailed Tyrant (*Culicivora caudacuta*), that are declining (Collar and Wege 1995, Stotz et al. 1996, Parker and Willis 1997).

We commend the Paraguayan government for having the foresight to establish San Luis and Cerro Corá national parks. We hope that our data will help underscore the importance of these parks, and that this information may be used in setting conservation priorities for the rapidly disappearing Cerrado.

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APPENDIX. Avian species and their relative abundance in Parque Nacional Serranía San Luis, depto. Concepción, Paraguay.

	Relative abundance[a]	Status[b]	Habitat[c]	Documentation[d]
Rhea americana[e]	U	P	1	P
Crypturellus undulatus	C	P	2	V
Crypturellus parvirostris	C	P*	1	C,V
Rhynchotus rufescens	U	P	1	V
Nothura maculosa	C	P		S
Phalacrocorax brasilianus	R	V	4	S
Syrigma sibilatrix	R	P*	1	C
Ardea alba				L
Bubulcus ibis	C	V	1	S
Butorides striatus				L
Nycticorax nycticorax				L
Plegadis chihi	C	V	1	S
Theristicus caudatus	U	P*	2	C
Mycteria americana	R	V	4	S
Coragyps atratus	U	P	2	S
Cathartes aura	U	P	2	S
Sarcoramphus papa	U	P	3	S
Cairina moschata	R	P	1	S
Leptodon cayanensis	R	P	3	C
Elanus leucurus	R	P	1	S
Rostrhamus sociabilis	R	AM	1	S
Ictinia plumbea	R	B	2	S
Accipiter bicolor	U	P	2	C
Buteogallus meridionalis	X	P	1	S
Harpyhaliaetus coronatus	X	P	2	S
Buteo magnirostris				L
Spizaetus ornatus	R	P	3	S
Caracara plancus	U	P	1	S
Milvago chimachima	R	P	1	L
Herpetotheres cachinnans	R	P	2	L
Micrastur ruficollis				L
Falco sparverius	R	P	1	L
Crax fasciolata	U	P	3	V
Aramides cajanea				L
Porzana albicollis				L
Cariama cristata	U	P	1	P
Vanellus chilensis	U	Pn	1	P
Rostratula semicollaris	X	V?	1	S
Tringa solitaria				L
Calidris fuscicollis				L
Gallinago paraguaiae				L
Columba cayennensis	C	P	3	V
Columbina squammata	U	P	1	S
Columbina talpacoti	C	P	1	V
Columbina picui	X	P*	1	C
Claravis pretiosa	C	P*	2	C,V
Leptotila verreauxi	C	P	1	S
Leptotila rufaxilla	U	P*	3	C
Anodorhynchus hyacinthinus	X	P	2	S
Ara chloropterus				L
Ara maracana				L
Aratinga leucophthalmus	C	P*	3	C,V
Aratinga aurea				L
Pyrrhura frontalis	C	P	3	C,V
Brotogeris chiriri				L
Pionus maximiliani	U	P	2	S
Amazona aestiva	U	P	3	V

APPENDIX. Continued.

	Relative abundance[a]	Status[b]	Habitat[c]	Documentation[d]
Coccyzus melacoryphus	U	B*	2	C
Piaya cayana	U	P	2	L
Tapera naevia	U	P	2	V
Crotophaga major	R	B	2	L
Crotophaga ani	C	P	1	V
Guira guira	C	P	1	V
Otus atricapillus	U	P*	3	C
Otus choliba	U	P	2	S
Pulsatrix perspicillata				L
Bubo virginianus				L
Glaucidium brasilianum	U	P*	2	C,V
Speotyto cunicularia	U	Py	1	P
Lurocalis semitorquatus	C	P?	3	V
Chordeiles minor				L
Podager nacunda				L
Nyctidromus albicollis	U	P*	2	C,V
Caprimulgus rufus	U	P*	3	C,V
Caprimulgus parvulus	U	P*ny	1	C
Nyctibius griseus	U	P*	2	C,V
Chaetura meridionalis[f]	U	IM	4	C,V
Thalurania furcata	R	P	3	C
Hylocharis chrysura	U	P	2	C,V
Trogon curucui	U	P	3	V
Momotus momota	R	P*	3	C,V
Baryphthengus ruficapillus	U	P*	3	C
Chloroceryle americana	R	P	2	S
Chloroceryle inda	R	P	2	S
Nystalus chacuru	R	P	2	V
Nystalus maculatus	R	P	2	C
Pteroglossus castanotis				L
Ramphastos toco	R	P	2	V
Picumnus cirratus	X	P	2	S
Melanerpes candidus	U	P	2	V
Picoides mixtus				L
Veniliornis passerinus	R	P	2	C,V
Piculus chrysochloros	R	P	3	S
Colaptes campestris	R	P	1	L
Celeus lugubris	R	P*	3	C
Dryocopus lineatus	R	P	2	L
Campephilus melanoleucos	R	P	3	L
Furnarius rufus				L
Schoeniophylax phryganophila	U	P	2	C,V
Synallaxis albescens	X	P	1	L
Phacellodomus rufifrons	X	P*	2	C
Philydor dimidiatus	R	P*	3	C,V
Philydor lichtensteini	U	P*	3	C,V
Philydor rufus	U	P*	3	C,V
Sittasomus griseicapillus	C	P*	3	C,V
Xiphocolaptes major	R	P*	2	C,V
Dendrocolaptes platyrostris	U	P*	3	C,V
Lepidocolaptes angustirostris	U	P*	2	C,V
Thamnophilus caerulescens	C	P*	3	C,V
Herpsilochmus atricapillus	U	P	3	C,V
Camptostoma obsoletum	U	P?y	2	C,V
Phaeomyias murina	U	B	2	V
Suiriri suiriri				L
Myiopagis caniceps	U	P?	3	S
Myiopagis viridicata	U	P?*	3	C,V
Elaenia flavogaster	U	P	2	V

APPENDIX. Continued.

	Relative abundance[a]	Status[b]	Habitat[c]	Documentation[d]
Elaenia albiceps	R	AM	2	C
Elaenia parvirostris	X	P?	2	S
Inezia inornata	R	P?*	2	C,V
Leptopogon amaurocephalus	U	P*	3	C,V
Corythopis delalandi	U	P*	3	C,V
Myiornis auricularis				L
Hemitriccus margaritaceiventer	U	P	2	C,V
Tolmomyias sulphurescens	U	P*	3	C,V
Platyrinchus mystaceus	C	P*	3	C,V
Myiophobus fasciatus	X	P?		S
Contopus cinereus	R	Pn	2	L
Lathrotriccus euleri	U	P?*	3	C,V
Cnemotriccus fuscatus	U	P?*	3	C,V
Pyrocephalus rubinus		P*		L
Xolmis cinerea	U		1	C
Xolmis velata	U	P*	1	C
Hymenops perspicillatus				L
Fluvicola leucocephala				L
Alectrurus tricolor	X	P?*	1	C
Gubernetes yetapa	U	P*	1	C,V
Machetornis rixosus	U	P*	1	C,V
Casiornis rufa	R	P	3	C,V
Sirystes sibilator	U	P*	3	C,V
Myiarchus swainsoni	U	P?*	3	C,V
Myiarchus tyrannulus	C	P*	2	C,V
Pitangus sulphuratus	U	Pn	2	S
Megarynchus pitangua				L
Myiodynastes maculatus	C	B*	2	C,V
Legatus leucophaius	U	B	2	V
Empidonomus varius	U	B	2	L
Griseotyrannus aurantioatrocristatus	U	B	2	C,V
Tyrannus melancholicus	C	By	1	L
Tyrannus savana	C	Bn	1	V
Xenopsaris albinucha	X	P?	3	S
Pachyramphus viridis	U	Pn	2	C,V
Pachyramphus castaneus	R	P	2	S
Pachyramphus polychopterus	R	Bn	2	V
Pachyramphus validus	R	P?n	2	V
Tityra cayana	R	P	3	S
Tityra inquisitor	U	P*	3	C,V
Pyroderus scutatus	U	P	3	C
Procnias nudicollis	R,C	P?*	3	C,V
Pipra fasciicauda	R	P	3	C
Oxyruncus cristatus	X	P	3	C
Progne chalybea	U	P?	1	L
Phaeoprocne tapera				L
Tachycineta leucorrhoa	R	B	1	S
Stelgidopteryx ruficollis	R	B	1	L
Cyanocorax cyanomelas	U	P	3	C,V
Cyanocorax cristatellus				L
Cyanocorax chrysops	X	P	3	C
Troglodytes aedon	C	P	2	V
Polioptila dumicola	R	P	2	C,V
Turdus rufiventris	U	P*	2	C,V
Turdus albicollis	C	P*	3	C,V
Turdus amaurochalinus	U	P	2	L
Catharus fuscescens	X	NM	3	C
Minus saturninus	U	P	1	L

APPENDIX. Continued.

	Relative abundance[a]	Status[b]	Habitat[c]	Documentation[d]
Mimus triurus				L
Vireo olivaceus chivi	C	P?*	3	C,V
Cyclarhis gujanensis	U	P	2	V
Parula pitiayumi	U	P	3	V
Geothlypis aequinoctialis	R	P	1	V
Basileuterus flaveolus	U	P*	3	C,V
Basileuterus hypoleucus	C	P*y	3	C,V
Conirostrum speciosum				L
Euphonia chlorotica				L
Thraupis sayaca	C	P	2	V
Eucometis penicillata	R	P*	3	C,V
Tachyphonus rufus	X	P*	2	C
Piranga flava	U	P	2	L
Trichothraupis melanops	R	P*	3	C
Cypsnagra hirundinacea				L
Nemosia pileata	U	P	3	V
Hemithraupis guira	U	P*	3	C,V
Saltator similis	U	P*	2	C,V
Saltator atricollis	U	P*	1	C,V
Paroaria coronata	X	P	2	S
Coryphospingus cucullatus	C	P*	2	C,V
Arremon flavirostris	R	P*	3	C,V
Volatinia jacarina	C	P	1	S
Sporophila plumbea	U	P?	1	C,V
Sporophila collaris				L
Sporophila caerulescens	C	P?	1	C
Sporophila bouvreuil	R	P*	1	C
Sporophila hypoxantha	X	P?	1	C
Sporophila ruficollis	U	P?	1	C
Sicalis flaveola	X	P	1	S
Embernagra platensis				L
Emberizoides herbicola	C	P*	1	C,V
Ammodramus humeralis	C	P*	1	C,V
				S
Zonotrichia capensis	R	P	1	S
Gnorimopsar chopi	C	P	1	V
Pseudoleistes guirahuro				L
Leistes superciliaris				L
Molothrus bonariensis	U	P*	1	C
Molothrus rufoaxillaris	U	P*	1	C,V
Scaphidura oryzivora			2	L
Icterus cayanensis	U	P	2	C,V
Cacicus chrysopterus	U	P*		C,V
Psarocolius decumanus	U	Pn	2	V
Carduelis magellanica	U	P	1	S
Passer domesticus	R	P	1	S

[a] Relative abundance criteria based on our work: X = single observation; R = rare, not recorded daily when in appropriate habitat, and only in small numbers when recorded, <5 individuals/day; U = uncommon, recorded in small numbers daily when in appropriate habitat, 1–10 individuals/day; C = common, recorded daily in large numbers when in appropriate habitat, >10 individuals/day.

[b] Status: P = permanent resident; a breeder with at least a few individuals present throughout the year. Most species given this designation are not known to make seasonal movements; virtually all with P? are presumed to have Austral migrant populations present at appropriate seasons; B = breeder only, Austral migrant; * = at least one individual/species had enlarged gonads indicative of breeding, n = nest found, y = young observed; V = visitor; nonbreeder, but may breed in adjacent areas to the park; IM = Intratropical migrant; AM = Austral migrant; NM = Nearctic migrant. Migrant terminology follows Hayes (1995b); ? = status uncertain. Hayes et al. (1994) and Chesser (1997) were consulted for Austral migrant status.

[c] Habitat based on our work: 1 = open grassland (campo); 2 = isolated woodlots in grassland, forest edge; 3 = forest; 4 = aerial.

[d] Documentation: C = collected; V = voice recorded; P = photographed; we use this designation only when a species was photographed but not "C" or "V". S = sight observation(s) only. L = based on specimens by the Kreig expedition to this region; referenced in Lauhmann (1939, 1940); see Methods for explanation.

[e] Species in boldface are threatened or near-threatened (Collar et al. 1992, 1994).

[f] Following Marín (1997).

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NOTES ON THE AVIFAUNA OF TABASCO

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ABSTRACT.—Tabasco, a Mexican state nearly half the size of the country of Costa Rica, lies juxtaposed between the Isthmus of Tehuantepec and the Yucatan Peninsula. This state hosts a diverse Neotropical resident avifauna, is a significant wintering area for Nearctic-Neotropic migrants, and has important biogeographic significance. Surprisingly little recent ornithological study has occurred in Tabasco; the last major publication treats data from 1939. Field work in March 1996 and recent specimens add nine species to the state list: *Caprimulgus vociferus, Chaetura vauxi, Campylopterus excellens, Empidonax albigularis, Thryothorus modestus, Turdus infuscatus, Myadestes unicolor, Limnothlypis swainsonii,* and *Vermivora ruficapilla.* The status of 26 other species is discussed. Further evidence of lowland forests being used as temporary refugia by birds from higher elevations is also considered. *Received 20 May 1998, accepted 19 Nov. 1998.*

"Compared to many of the Mexican States, Tabasco has been slighted ornithologically. Anything collectors could obtain in Tabasco could also be found in southern Veracruz with less effort. If the collector were to exert the effort necessary to enter Tabasco, he might as well go the entire distance and travel on to the Yucatan Peninsula, an area with many unique and peculiar forms." Berrett (1962:4).

Tabasco, a state of approximately 24,600 km^2, is situated on the northeastern side of the Isthmus of Tehuantepec on the Gulf of Mexico (Fig. 1). The ornithological neglect of Tabasco noted by Berrett (1962) has generally continued for the past 35 years. Berrett (1962) added 166 species to those previously known from Tabasco and reported a total of 457 species from the state. The bibliographic and museum database research of Centeno (1994) added 73 species to the total reported by Berrett (1962), but the knowledge of avian distribution within Tabasco and specimen representation of the birds of the state remain relatively poor. Avian specimens apparently do not even exist from 3 of the state's 17 municipios (the equivalent of counties in the U.S.A.; Centeno 1994).

Perhaps because the two major works on Tabasco birds in the last 55 years are not readily available (Berrett 1962, Centeno 1994) and because specimen representation is sparse, errors and omissions regarding the distribution and occurrence of birds in the state have been fairly common (e.g., Peterson and Chalif 1973, Howell and Webb 1995). The last major publication on the birds of Tabasco is the outdated report by Brodkorb (1943), which was based on a collection made in the region by the botanist Eizi Matuda and his assistants in 1939.

In this paper we report on our recent efforts to increase existing knowledge of the birds of Tabasco. In March 1996 we held a collaborative field workshop in the municipios of Centla and Huimanguillo. In Centla (the northeastern most municipio in the state, bordering Campeche), our field studies were conducted from 4–13 March on the Río Grijalva in the Reserva de la Biosfera Pantanos de Centla (Fig. 1). Our studies were focused mainly on two sites in the area of 18° 29′ N, 92° 38′ W. The first site was a remnant tract of mangrove (*Rhizophora mangle*) and puktal (*Bucida buceras*) forest (a selva perennifolia, or evergreen forest) along the banks of Arroyo Polo, a tributary of the Río Grijalva about 4 km south of Frontera. The other area was a partially flooded, shrubby pasture on the banks of the Río Grijalva and Río San Pedrito, about 14 km south of Frontera. Additional observations were made on water and land between these two sites.

In Huimanguillo, the southwesternmost

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FIG. 1. The Mexican state of Tabasco, with its capital city of Villahermosa and the location of our study sites at the Biosphere Reserve of Pantanos de Centla and near the ejido of Malpasito.

municipio (bordering Veracruz and Chiapas), our field studies were conducted from 14–22 March in the southwesternmost corner of the state, below Cerro La Pava, west of Ejido Malpasito, and approximately 5 km west of the state's border with Chiapas (ca 17° 20′ N, 93° 36′ W, 300–500 m elevation; Fig. 1). This site consisted of open fields, pastures, small fruit and coffee plantations, acahual (second growth forest), and remnant rainforest patches restricted to mountain crevices and arroyos.

In addition to specimens and observations obtained during our field work, we include some additional specimen-based information for the birds of Tabasco from the national ornithological collection of México (Colección Nacional de las Aves—CNAV), which is housed at the Instituto de Biología, Departamento de Zoología, Universidad Nacional Autónoma de México, in Mexico City. Our specimens representing new records for the state were also deposited in CNAV. A number of records we report as new for the state were predicted by Berrett (1962). Several of our records expand the known distribution of particular species within the state; many of these were also foreseen by Berrett (1962).

SPECIES ACCOUNTS

Broad-winged Hawk (Buteo platypterus).—Berrett (1962) recorded only two observations of this species in Tabasco, both of migratory flocks (28 March 1960, 17 April 1961). What appears to be the first state specimen, a female in migration, was taken at Balneario Agua

Blanca, Macuspana, on 13 March 1989 (CNAV 13,523).

Ruddy Crake (Laterallus ruber).—Berrett (1962) noted that the species had been reported from only two areas in the state (near Tenosique and Teapa), but that it was probably more widespread. We found the species to be very common at Pantanos de Centla, hearing its distinctive vocalizations daily during our stay in the area.

Common Snipe (Gallinago gallinago).—Berrett (1962) reported few Tabasco records of this wintering migrant, including only three sightings of his own. All but one of the records (from Sánchez Magallanes) were from southern, inland areas of the state. We observed at least one individual per day at Pantanos de Centla on 8–10 March.

Sandwich Tern (Sterna sandvicensis).—Berrett (1962) reported collecting the first specimens for the state at Sánchez Magallanes and Miramar; his observations of the species did not extend beyond these areas. We found this tern to be common on the Río Grijalva from Frontera to an area about 5 km to the south. Two to approximately 40 individuals were seen almost daily during our stay in this area.

Least Tern (Sterna antillarum).—Berrett (1962) reported only a single specimen from the state taken by D. M. Lay on 2 May 1960 near Jonuta on the Río Usumacinta. Apart from the many individuals Lay observed near Jonuta on 6 April and 2 May 1960, only two other observations (both of single individuals) were reported by Berrett: one from Chablé on the Río Usumacinta and the other from near Chontalpa (Huimanguillo) on the Río Grijalva. These are all inland records. On 12 March at Pantanos de Centla we had the opportunity to closely observe approximately 40 individuals feeding over the Río Grijalva near Frontera in loose aggregation with individuals of the preceding species.

Mangrove Cuckoo (Coccyzus minor).—Berrett (1962) noted few Tabasco records and felt that the species was restricted to coastal areas. We note a male taken from a decidedly inland locality 6 km S of Huimanguillo on 6 March 1984 by H. Muñoz (CNAV 2,904).

Common Parauque (Nyctidromus albicollis).—Berrett (1962) noted that his specimens of this permanent resident taken between 11 March and 7 May were in breeding condition. An individual found during the day in riverbank mangrove/selva forest on 5 and 6 March acted as though it was nesting when we flushed it. We did not find a nest, but on 7 March found a single egg laid on the leaf litter in one of our mist net lanes. We captured and banded the bird when it returned to this nest. A second egg was laid by 12 March (our next visit to the site).

Whip-poor-will (Caprimulgus vociferus).—New record. Berrett (1962) noted only a single report of this species from Tabasco, that of Rovirosa (1887). Rovirosa's observations are notoriously suspect, however; Brodkorb (1943:8) stated that " . . . scarcely any reliance can be placed on his records which have not been confirmed by other workers." In fact, Rovirosa (1887) simply pooled all of his caprimulgid observations under this single specific epithet, apparently not knowing what species he had observed and perhaps liking this particular name. Under "*Antrostomus vociferus*" he stated that various species of caprimulgid occurred in the state from January to May. Thus, based on present evidence (i.e., Berrett 1962), it seems likely that Rovirosa was discussing one or more of the four other caprimulgids that have since been found to occur in the state. Given its commonness and vocal habits, his observations probably consisted mostly of *Nyctidromus albicollis,* but this is speculative, and does not explain his lack of records from the second half of the year.

KW distinctly heard a Whip-poor-will singing at Pantanos de Centla on 9 March. The song was of the "Mexican" subspecific group (*C. v. arizonae/oaxacae/chiapensis*), which Howell and Webb (1995) suggested might occur in lowlands during the nonbreeding season. Subsequently, we discovered that a specimen of this subspecies group had been taken on 16 March 1984, 10 km S of Chontalpa, Municipio de Huimanguillo, by F. Ornelas (CNAV 2,917).

Vaux's Swift (Chaetura vauxi).—New Record; no specimen. A flock of approximately 15 individuals was seen and heard at close range above Malpasito, Huimanguillo on 15 March, and a flock of 35–40 was seen each day 16–18 March. The first migrant *Chaetura pelagica* of the spring (a species that might be

confused with *C. vauxi*) were seen and heard on 21 March.

Violet Sabrewing (Campylopterus hemileucurus).—The four specimens recorded by Berrett (1962) for the state all came from near Teapa. The single additional sight record noted was from near Chontalpa. We collected two females on 17 and 19 March at Malpasito. Neither had yet entered reproductive condition.

Long-tailed Sabrewing (Campylopterus excellens).—New Record. An adult female of this species was taken at Malpasito in remnant forest at the edge of a small arroyo. This is the first record of this species for the state, and also the northeasternmost occurrence of the species, which until recently has been considered to have a very restricted range (see Winker et al. 1992a, Howell and Webb 1995). Howell and Webb (1995) based their extension of the species' range into Chiapas on a previously misidentified specimen in the American Museum of Natural History. Reexamination of this specimen (KW) suggests that Howell and Webb (1995) were correct; it is a *Campylopterus excellens,* and not a *C. curvipennis* as originally identified. Together, these two specimens suggest an approximate doubling of the species' total geographic range.

Pygmy Kingfisher (Chloroceryle aenea).—Hitherto, the only records for this species in the state were from southern, inland localities (Balancán and Ocuápan: Berrett 1962; Chontalpa: CNAV 2,933). We collected a nonbreeding female at Pantanos de Centla on a small, well-forested tributary (Arroyo Polo) of the Río Grijalva on 6 March.

Wedge-billed Woodcreeper (Glyphorhynchus spirurus).—Recorded by Berrett (1962) as an uncommon resident of the rainforest belt of the state, records were lacking from the westernmost rainforest in the state (Municipio de Huimanguillo). We collected a nonbreeding female in a patch of acahual (second growth forest) at the base of the local mountains at Malpasito on 17 March.

Ochre-bellied Flycatcher (Mionectes oleagineus).—Although Berrett (1962) recorded this species near Chontalpa, he did not find it to be particularly common. We found it to be rather common at Malpasito, collecting seven individuals 19–21 March. Their abundance at the site was associated with the weather; they were undetected before a relatively cold norte (cold, wet weather system from the north) arrived on 19 March.

Sepia-capped Flycatcher (Leptopogon amaurocephalus).—A male taken on 20 March at Malpasito (testes moderately enlarged) extends the range of this species within the state to the westernmost occurrence of the rainforest belt.

Sulphur-rumped Flycatcher (Myiobius sulphureipygius).—As with the previous species, Berrett (1962) documented this species as a permanent resident of the rainforest belt, but lacked records for the westernmost rainforest in the state. We collected a male with unenlarged testes in acahual at Malpasito on 20 March.

White-throated Flycatcher (Empidonax albigularis).—New Record. We collected what appear to be the first specimens for the state at Pantanos de Centla on 10 March in a shrubby pasture. Both birds were males with no fat and a heavy molt that included body, wings, and tail.

Great Crested Flycatcher (Myiarchus crinitus).—Berrett (1962) noted a single specimen and a few sightings of this species in Tabasco, all from May 1961 and near Balancán. We note two other specimens, both males, taken on 13 March 1984 and 29 September 1965 (indicating a presence in fall migration as well as spring), near Comalco and on the Río San Pablo, Municipio de San Pablo by F. Ornelas and R. W. Dickerman, respectively (CNAV 3,491 and 17,215).

Gray-collared Becard (Pachyramphus major).—An adult male, apparently the second specimen for the state (Berrett 1962), was taken in 8–10 m acahual on 20 March at Malpasito. The first specimen, also a male, was taken in the eastern part of the state near Reforma, Balancán, on 28 May 1939 (Brodkorb 1943).

Mangrove Vireo (Vireo pallens).—Berrett (1962) collected the only previous specimen for the state (male, 13 April 1961) near Villahermosa and noted three additional sightings: two near Villahermosa and another on the Río Usumacinta at Emiliano Zapata (all in April 1961). Peterson and Chalif (1973) and Howell and Webb (1995) overlooked these records. We collected two more individuals in low-

lying, shrubby pasture on the Río Grijalva at Pantanos de Centla on 9 and 10 March. Both were females with no fat and unenlarged ovaries. At least one more individual was later seen in this same area.

Blue-headed Vireo (Vireo solitarius).—Berrett (1962) reported only two observations of this species in the state (March 1959, March 1960), both near Teapa. We collected what are apparently the first two state specimens at Malpasito on 16 and 17 March, a female with no fat and a male with little fat.

Green Jay (Cyanocorax yncas).—Berrett (1962) recorded specimens and sightings of this species from only four localities in the municipios of Balancán, Centla, and Teapa. Our sightings of two individuals each on 15 and 21 March at Malpasito indicate that the species also occurs in the western part of the state.

Tree Swallow (Tachycineta bicolor).—Berrett (1962) recorded only one specimen for the state but noted a few additional sightings, including several large flocks. Although it remains unclear whether the species spends the winter or is only a transient in migration, we add the following records from Pantanos de Centla: three specimens, all females with little fat, taken on 8 March 1996, and sightings of 1–150 individuals almost daily from 4–12 March. In addition, a female was taken by R. W. Dickerman 53 km W of Villahermosa on 3 April 1973 (CNAV 17,723).

Plain Wren (Thryothorus modestus).—New record. An adult female was taken at Balneario Agua Blanca, Macuspana, in selva mediana, by E. Diaz I. on 14 March 1989 (CNAV 13,389).

Slate-colored Solitaire (Myadestes unicolor).—New record. We collected a male on 20 March at Malpasito during the same norte associated with the occurrence of the Black Robin (below) in the area. Movement of Slate-colored Solitaires to lowland forest during nortes is a frequent occurrence in the Sierra de Los Tuxtlas in southern Veracruz (Ramos 1983; KW, pers. obs.).

Black Robin (Turdus infuscatus).—New record; no specimen. A female or immature male of this highland species was seen feeding in a fruiting tree on 20 March at Malpasito on the last day of a relatively cold norte. It had probably descended to this lower elevation (ca 450 m) to escape less suitable conditions in the highlands, a common occurrence in some areas of southern Mexico (see Winker et al. 1992b).

White-throated Robin (Turdus assimilis).—Berrett (1962) noted only three records of this species in Tabasco, one specimen and two sightings from near Teapa and near Chontalpa, both southern localities. A male was taken at Comalcalco (in the northern part of the state) on 13 March 1984 by F. Ornelas (CNAV 6,776).

Nashville Warbler (Vermivora ruficapilla).—New record. Berrett (1962) reported a brief glimpse of a bird that was probably this species at Balancán. We collected the first state specimen, a female with no fat, at Malpasito on 20 March.

Yellow-rumped Warbler (Dendroica coronata).—Berrett (1962) reported only a few records for this species, all from December. Weber (1945) reported it at La Venta in spring 1943. We took three females with moderate to heavy fat in shrubby pasture at Pantanos de Centla on 9–11 March, and observed up to three other individuals on these days.

Swainson's Warbler (Limnothlypis swainsonii).—New record. The first state specimen, a male with no fat and with tail characteristics (uneven growth bars) of an after second year (ASY) individual, was taken in a mixed forest of mangrove and selva near the bank of Arroyo Polo (Río Grijalva) near Frontera on 6 March. This bird was not in migratory condition and the habitat it occupied was eminently suitable for wintering (KW, pers. obs.; see Graves 1998).

White-winged Tanager (Piranga leucoptera).—Berrett (1962) reported a few individuals of this species in early and mid-November 1961 near Tenosique and surmised that they may have been wintering birds from higher elevations. We saw a single female at Malpasito on 19 March, during the same norte associated with the presence of the Black Robin and Slate-colored Solitaire noted above.

Orange-billed Sparrow (Arremon aurantiirostris).—Berrett (1962:375) noted six specimens from the state and referred to the species as a "rarely recorded permanent resident of the humid rain forest undergrowth." Although we worked intensively in the Malpasito area

for four days before encountering any individuals of this species, during the relatively severe norte of 19 and 20 March we collected four individuals (three females, one male) in our mist nets that had been in the same locations the entire time in a small patch of remnant rainforest at the base of the local mountains. This striking movement pattern of increased captures during nortes is typical of highland species at lowland sites, but not of lowland species. We surmise that at this site these typically lower-elevation birds might occupy less disturbed forest at slightly higher elevations than the remnant forest available where our field work was conducted.

Olive Sparrow (Arremonops rufivirgatus).—Berrett (1962) reported only a single specimen, but noted that the species was a common permanent resident north of Balancán. These records were overlooked by Howell and Webb (1995). We found that the species also occurs in the westernmost region of the state. We collected a female with an unenlarged ovary on 18 March at Malpasito and, in addition, found what appeared to be two pairs (two singing males with associated individuals not singing) in a brushy area of young second growth.

Savannah Sparrow (Passerculus sandwichensis).—Four individuals were seen on 14 March beside scrubby pasture at Pantanos de Centla on the Río Grijalva, supplementing the single specimen and several sightings reported by Berrett (1962) from a southern part of the state (Huastecas, Teapa, ca 29 km NE of Teapa).

Lincoln's Sparrow (Melospiza lincolnii).—Berrett (1962) included this species as an uncommon wintering bird in the state, reporting only a single specimen and scattered sight records from largely southern, inland sites. Our records add northern, near-coastal records for the state. We observed a single individual on 4 March at Pantanos de Centla in roadside scrub, and collected a male with light fat on 11 March in shrubby pasture on the Río Grijalva.

DISCUSSION

Our records consist of 10 migrant and 25 resident species. Of our nine new records for the state, only two are of migrant species; seven are resident. This is unusual for an area in the northern Neotropics, where at the end of the twentieth century one would expect our knowledge of the avifauna to be sufficiently strong that most new records would be generated by individuals of migrant species. We consider the preponderance of resident species in this report to be a reflection of Tabasco's status as a poorly known Neotropical region. Further ornithological study of this region is fully warranted. Tabasco is nearly half the size of Costa Rica. It occupies a geographic position making it important as a wintering ground for Nearctic-Neotropic migrants and as a breeding and nonbreeding area for a diverse Neotropical resident avifauna. Further, it has twofold biogeographic significance: one as a transition zone between the Yucatan Peninsula and the Isthmus of Tehuantepec (including a significant portion of the rainforest belt at the peninsula's base) and another in its position at the northern limits of Neotropical families such as Heliornithidae, Eurypygidae, Galbulidae, Bucconidae, and Pipridae.

Our data provide important new distributional information for both resident and migrant species in this poorly known region. For example, our records of Swainson's Warbler and the Long-tailed Sabrewing constitute significant wintering and probable breeding range extensions (respectively) for rare species of conservation concern (see Howell and Webb 1995, Winker et al. 1992a).

In addition, our data show intermittent use of lowland forest, indicating movements among "resident" birds. The relatively lowland sites we studied near Malpasito suddenly became home to individuals of a number of species that were not detected during the four days of intensive field study prior to the arrival of a norte on 19 March. At least five species (including two new to the state) showed movement patterns that were strongly tied to the inclement weather: *Mionectes oleagineus, Turdus infuscatus, Myadestes unicolor, Piranga leucoptera,* and *Arremon aurantiirostris.* All of these species probably occupy forest at higher elevations in this area. An increase in overall capture rates and census detections (unpubl. data) suggested increased numbers of individuals of many species already present at the lowland sites. These individuals may also have come from the local highlands.

Temporary use of remnant lowland forest

during nortes is a relatively common phenomenon in southern Veracruz (Ramos 1983, Winker et al. 1997) and is an issue of grave conservation concern; when lowland forests have diminished to a degree of scarcity, they are no longer available to individuals seeking temporary refuge from inclement conditions in the highlands.

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PREDATION OF SMALL EGGS IN ARTIFICIAL NESTS: EFFECTS OF NEST POSITION, EDGE, AND POTENTIAL PREDATOR ABUNDANCE IN EXTENSIVE FOREST

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ABSTRACT.—After photographic observations in the field and laboratory tests indicated that small rodents might be significant predators on small eggs, we conducted a field study in central Massachusetts to compare predation of House Sparrow (*Passer domesticus*) eggs in artificial nests near to (5–15 m) and far from (100–120 m) forest edges and between ground and shrub nests. As in earlier studies in managed northeastern forest landscapes that used larger quail eggs, predation rates on small eggs in nests at the forest edge did not differ ($P > 0.05$) from those in the forest interior for either ground nests (edge = 0.80 vs interior = 0.90) or shrub nests (edge = 0.38 vs interior = 0.28) after 12 days of exposure. However, predation rates on eggs in ground nests were significantly higher ($P < 0.001$) than in shrub nests at both the edge and interior. There were no significant ($P > 0.05$) differences in the frequency of capture of the 6 most common small mammal species between forest edge and interior. Logistic regression analyses indicated a highly significant ($P < 0.001$) nest placement effect but very little location or small mammal effect. Predation of small eggs by small-mouthed ground predators such as white-footed mice (*Peromyscus leucopus*) has not been documented as a major factor in egg predation studies, but use of appropriately-sized eggs and quantification of predator species presence and abundance seems essential to future studies. *Received 31 March 1998, accepted 5 Jan. 1999.*

Previously published evidence for elevated nest predation rates at forest edges in the northeastern U.S. is not consistent. For example, in Maine, predation rates were higher for artificial nests placed in shrubs at edges than in forest interiors, but the distance to edge had no effect on predation of ground nests (Rudnicky and Hunter 1993). Also, neither the edge:area ratio of forest patches nor the distance from edge affected artificial ground nest predation rates (Small and Hunter 1988). Predation rates of artificial nests were higher in extensive industrial forests than in fragments, but within fragments, shrub nests near edges were depredated at a higher rate than those farther from edges. Furthermore, the predation rate in clearcuts was lower than that in forest fragments or plantations, and within plantations, predation rates increased with increasing distance from the edge (Vander Haegen and DeGraaf 1996). In Pennsylvania, Yahner and Scott (1988) reported a direct relationship between amount of forest fragmentation caused by clearcutting and predation rates on artificial nests, yet Yahner and coworkers (1993) did not find greater predation rates on such nests despite greater fragmentation resulting from additional clearcutting on the same study area. In sum, the results of previous studies in the northeastern U.S. are inconsistent, perhaps because the large quail (*Coturnix* sp.) or chicken (*Gallus* sp.) eggs used do not sample the entire predator community (Haskell 1995). Would the use of eggs of approximately the same size as most forest passerines shed light on patterns of predation on artificial nests in relation to forest edge?

White-footed mice (*Peromyscus leucopus*) were frequently recorded by remotely-triggered cameras at ground and shrub nests containing eggs of Japanese Quail (*Coturnix japonica*); many of these same nests appeared to be undisturbed at the end of the exposure period and thus were not classified as visited by predators (Danielson et al. 1997). Similarly, Northern Bobwhite (*Colinus virginianus*) eggs at artificial nests in Minnesota that were visited (as determined by photographs) by red-backed voles (*Clethrionomys gapperi*) and deer mice (*Peromyscus maniculatus*) were not damaged, although those nests were classified as depredated by Fenske-Crawford and Niemi (1997). Small mammalian predators are clear-

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ly able to locate artificial nests, but have limited ability to destroy quail eggs in these nests. Quail eggs are not representative of the sizes of eggs of most temperate forest passerines, especially those of Neotropical migratory species (Haskell 1995, DeGraaf and Maier 1996). If appropriately-sized eggs were not available to potentially common predators, then results of previous studies to estimate nest predation rates for forest songbirds may have been biased, contributing to the inconsistency of results in extensive northeastern forests.

Egg size is potentially important in nest predation studies; even though small rodents such as mice and eastern chipmunks (*Tamias striatus*) may be egg predators (e.g., Maxon and Oring 1978, Reitsma et al. 1990, respectively), they apparently cannot readily open and consume the larger eggs of quails and chickens (Roper 1992, Haskell 1995; but see Craig 1998). Roper (1992) showed that predators did not respond to quail eggs as they did to native birds' eggs in Panama because most mammalian nest predators were too small to eat quail eggs. Such eggs, however, are virtually the only ones that have been used in artificial nest predation studies (Major and Kendal 1996).

These facts led us to conduct a laboratory experiment of mouse predation on large (*C. japonica*) and small (Zebra Finch, *Taeniopygia guttata*) eggs (DeGraaf and Maier 1996). Mouse predation on small eggs was immediate but did not occur on the large eggs. Similar laboratory trials (Maier and DeGraaf, unpubl. data) indicated that white-footed mice, including juveniles, could open House Sparrow (*Passer domesticus*) eggs; we conducted a field study to evaluate egg predation in artificial nests containing such eggs.

We attempted to assess the effects of nest location (edge vs interior), placement (shrub vs ground), and the relative abundance of small mammals on the predation of small eggs. We hypothesized that small mammals were equally abundant at edges and in forest interiors (Heske 1995), that no edge-related differences in nest predation would be found for either ground or shrub nests (Major and Kendall 1996), and that predation would be greater on ground nests than on shrub nests because small mammals such as mice and chipmunks spend the majority of their foraging time on the ground (Madison 1977, Elliot 1978, Graves et al. 1988).

METHODS

We placed artificial nests near (5–15 m) and far (100–120 m) from stand edges in 40 mature stands in an extensive managed mixed-wood forest in central Massachusetts during June to 15 July 1997. All stands were at least 80 years old and of the red oak (*Quercus rubra*)-white pine (*Pinus strobus*)-red maple (*Acer rubrum*) forest-cover type (Eyre 1980); edges were formed by small (2–4 ha) clearcuts 1–6 years old. We placed two ground nests and two shrub nests in each stand, one of each type near and far from the edge and at least 100 m from each other (Fig. 1). Nests (160 total) were wicker baskets 10 cm in diameter and 6 cm deep, weathered for 3 weeks before use, and contained one fresh House Sparrow egg. To minimize human scent at nests, we wore rubber boots and clean cotton gloves during nest placement (Whelan et al. 1994). Ground nests were set into the surface litter; shrub nests were wired 1–1.5 m above the ground in crotches or forks of branches of shrubs or small saplings. All nests were checked after 12 days, approximately the mean incubation time for small forest passerines. Eggs found out of the nest, destroyed in the nest, or missing were classified as predations.

We analyzed the nest predation data as paired-sample nest types within stands (Zar 1996:163) and performed statistical tests using SYSTAT 7.0 for Windows. Sign tests were used to detect differences in the number of nest predations among edge and interior nests on the ground and in shrubs (Zar 1996:536).

We assessed the relative abundance of small mammal species at edge and interior sites using 3-day removal trapping (Miller and Getz 1977) at each site immediately after the nest predation experiments. Two circular trapping arrays (20 traps/20 m diameter array) were set in each of the 40 stands, one midway between edge nests and one between interior nests (Fig. 1). Different types of small mammal traps are more efficient for trapping certain species under varying conditions, e.g., weather (Williams and Braun 1983, Bury and Corn 1987, Mengak and Guynn 1987); we used four types of traps in an attempt to more completely sample the small mammal community (Pelikan et al. 1977). Small Victor snap traps with expanded pedals, Museum Special snap traps with expanded pedals, large (approx. 8 × 8 × 24 cm) Sherman traps, and modified large Sherman live traps with circular glass windows (5.5 cm diameter) in the rear door were used at each array in equal numbers. All traps were baited with a mixture of peanut butter, oatmeal, bacon, and black sunflower seed and were checked daily. All small mammals collected were deposited in the Vertebrate Museum of the University of Massachusetts, Amherst, Massachusetts. We followed the guidelines for the capture and handling of mammals approved by the American Society of Mammalogists (American Society of Mammalogists 1998).

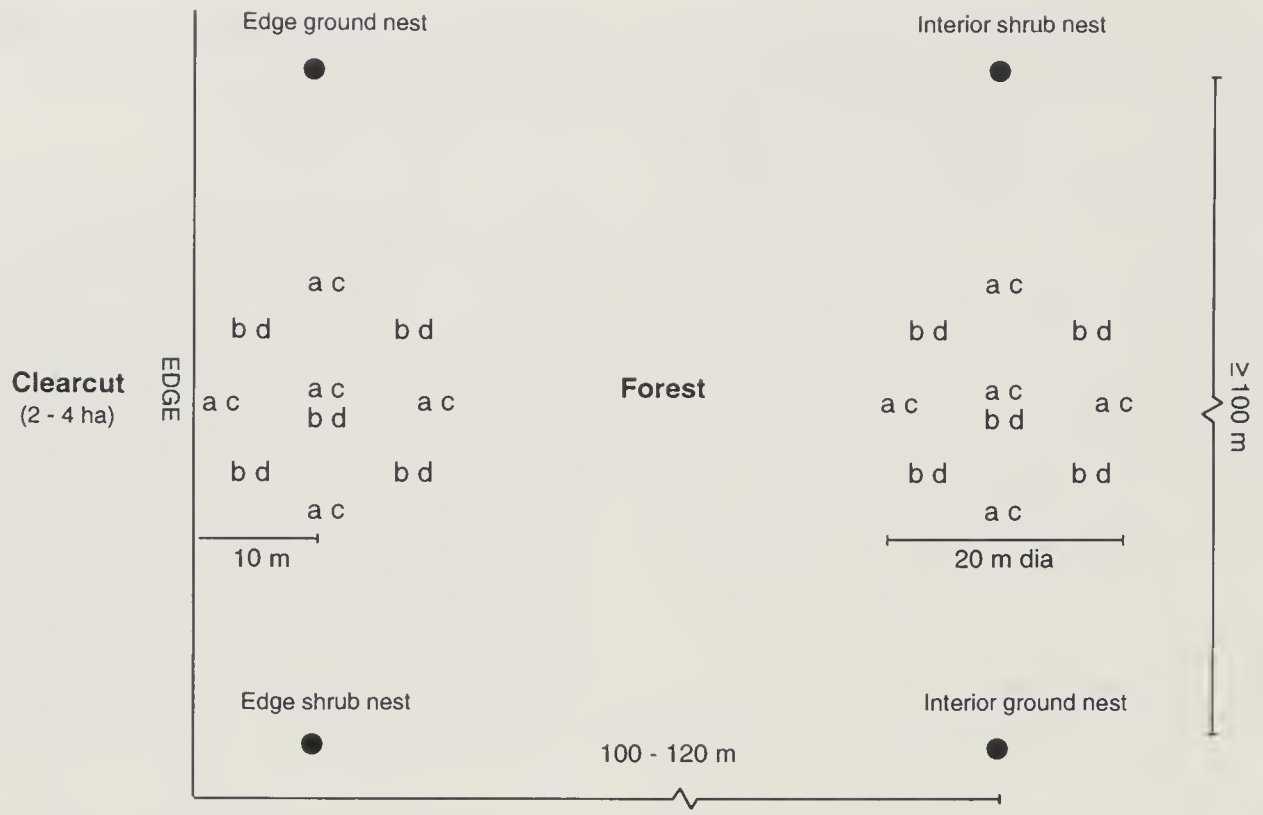

FIG. 1. Placement of small mammal trapping arrays and artificial nests in central Massachusetts, June–August, 1997. Four types of traps include: (a) small Victor snap, (b) Museum Special, (c) large Sherman, (d) large Sherman with glass window. (Figure not to scale.)

Small mammal capture counts were compared by species between edge and interior using the Wilcoxon paired-sample test for species with sufficient n (Zar 1996:167). Logistic regression (PROC LOGISTIC, SAS 1989) was used to assess the relationship between small mammal counts and nest predation; we used a model with nest placement (ground or shrub), location (edge or interior), and small mammal abundance effects; the first two were treated as categorical variables and the third as a continuous variable. The tests for whether a coefficient is zero were carried out using Z = (estimated coefficient/standard error) with the P-value obtained using the standard normal distribution (Hosmer and Lemeshow 1989:17).

RESULTS

We did not detect any significant differences between the number of nest predations at the forest edge and those in the forest interior for either ground nests (Sign test: ties = 28, 4 "+", 8 "−", critical value = 2, $P > 0.05$) or shrub nests (Sign test: ties = 24, 10 "+", 6 "−", critical value = 3, $P > 0.05$). However, the number of nest predations on ground nests at both the edge (Sign test: ties = 15, 21 "+", 4 "−", critical value = 7, $P < 0.001$) and interior (Sign test: ties = 15, 25 "+", 0 "−", critical value = 7, $P < 0.001$) were significantly higher than those on shrub nests.

Twelve species of small mammals were detected; six species represented 99% of captures at both forest edge and interior. The distributions of the 6 most commonly detected small mammal species did not differ significantly (Wilcoxon paired-sample tests: $P > 0.05$) between stand edges and interiors (Table 1). White-footed mice were detected more than all other species combined in both stand edges and interiors and were the only small mammal species detected in all 40 stands. Logistic regression analyses confirmed nest placement (ground, shrub) effects but showed no effect of small mammal abundance or location (edge, interior) on nest predation rate (Table 2).

DISCUSSION

Because this is the first study that we know of to systematically evaluate artificial nest predation in relation to forest edge using small eggs, comparison with other studies where larger eggs were used is difficult. In a recent review of studies in both agricultural and settled landscapes in North America and Europe, Major and Kendal (1996) showed that egg predation (on large eggs) was higher near the

TABLE 1. Numbers of small mammals captured near edges and interiors of 40 stands in extensive forest in central Massachusetts, July and August 1997. Wilcoxon paired-sample results for most commonly detected species; N = stands species detected in, n = differences (N minus ties), T = smallest sum of ranks, $T_{0.05(2),n}$ = critical value (Zar 1996: table B.12).

Species[a]	Edge	Interior	Total	N	n	T	$T_{0.05(2),n}$	P
White-footed mouse (*Peromyscus leucopus*)	251	235	486	40	34	262.5	182	>0.05
Red-backed vole (*Clethrionomys gapperi*)	74	63	137	25	21	90.5	58	>0.05
Northern short-tailed shrew (*Blarina brevicauda*)	61	65	126	35	28	202.0	116	>0.05
Masked shrew (*Sorex cinereus*)	16	22	38	17	15	44.0	25	>0.05
Eastern chipmunk (*Tamias striatus*)	14	5	19	15	15	28.5	25	>0.05
Smoky shrew (*Sorex fumeus*)	7	3	10	9	9	13.5	5	>0.05

[a] Species detected in ≤3 stands: woodland jumping mouse (*Napaeozapus insignis*), flying squirrel (*Glaucomys* sp.), long-tailed weasel (*Mustela frenata*), red squirrel (*Tamiasciurus hudsonicus*), pine vole (*Microtus pinetorum*), meadow vole (*Microtus pennsylvanicus*).

forest edge in three studies, higher away from the edge in one study, and equal in seven studies. Predation of artificial nests containing Northern Bobwhite eggs in Wisconsin pine barrens savannah patches was correlated with proximity to the edge (Niesmuth and Boyce 1997). Predation on artificial nests containing small chicken, Japanese Quail, and plasticine eggs in Alberta was highest in larger woodlots and showed no edge effect (Hannon and Cotterill 1998). Two additional studies (which used Japanese Quail eggs) in the northeastern U.S. did not detect any difference in predation rates between edges and interiors of extensive-managed forests (Table 3; Vander Haegan and DeGraaf 1996) or suburban/agricultural/forest landscapes (Danielson et al. 1997). Along with our current results, these variable findings suggest either that the "edge" effect as related to egg predation (Andrén and Angelstam 1988) is not a widespread phenomenon or that not all forest edges are the same; i.e., forest-clearcut, forest-agriculture, and forest-suburb edges differ in the predators present (Danielson et al. 1997).

Equally variable are the results of nest placement studies (i.e., ground vs shrub/elevated nests). Major and Kendal (1996) reported higher predation at elevated nests in six studies, higher predation at ground nests in four studies, and equal predation rates in three studies. Ground nests containing Japanese Quail and plasticine eggs had increased predation along farm edge and interior in Saskatchewan, but there were no detectable differences in predation rate between ground and shrub nests at logged edge, logged interior, or contiguous forest (Bayne and Hobson 1997). Although two studies in the northeastern U.S. did not detect any difference in predation rates between ground and shrub nests (Vander Haegan and DeGraaf 1996, Danielson et al. 1997), we found a strong placement effect (high predation on ground nests) using small eggs.

Where edge or nest placement effects occurred, generalist predators commonly were presumed to depredate specific nest types disproportionately. The variability in results among studies may reflect differences in nest predator guilds or the abundance of particular species in study areas (e.g., Picman 1988). Attempts to identify individual egg predators include characterizations of predation remains of real eggs (Gottfried and Thompson 1978, but see Marini and Melo 1998), impressions in plasticine (Bayne et al. 1997), and clay eggs (Donovan et al. 1997), hair catchers (Baker 1980), and remotely triggered cameras (DeGraaf 1995). Nevertheless, egg predation

TABLE 2. Parameter estimates and statistics from logistic regression analysis of placement (ground/shrub), location (edge/interior), and small mammal abundance in relation to predation of small eggs in artificial nests in central Massachusetts, 1997. The tests for whether a coefficient is zero were carried out using Z = (est. coefficient/SE) with the P-value obtained using the standard normal distribution (equivalent to $C = Z^2$ with the P-value based on χ^2 distribution with 1 df).

Variable	Estimated coefficient	Standard error	P
INTERCEPT	−1.7320	0.5080	0.0007
LOCATION	0.0002	0.3805	0.9996
W-F MICE	−0.0005	0.0602	0.9940
PLACEMENT	2.4655	0.3937	0.0001

TABLE 3. Predation rates (%) on eggs in artificial nests exposed for 12–14 days at forest edge and interior (>50 m) in the northeastern U.S.

Nest placement	Egg size	Edge		Interior			Study location	Reference
		Rate	*n*	Rate	*n*	*P*		
Ground	Sparrow	0.80	40	0.90	40	>0.05	Massachusetts	This study
	Quail	0.45	20	0.41	80	>0.05	Massachusetts	DeGraaf, unpubl. data[a]
		0.20	50	0.25	48	>0.05	Maine	Vander Haegan and DeGraaf 1996[b]
		0.29	42	0.21	42	>0.05	Maine	Rudnicky and Hunter 1993
Shrub	Sparrow	0.38	40	0.28	40	>0.05	Massachusetts	This study
	Quail	0.60	20	0.51	80	>0.05	Massachusetts	DeGraaf, unpubl. data[a]
		0.16	50	0.14	50	>0.05	Maine	Vander Haegan and DeGraaf 1996[b]
		0.55	42	0.29	42	0.015	Maine	Rudnicky and Hunter 1993

[a] Recalculated from data used by Danielson et al. 1997.
[b] From Table 1; edge = 5 m and interior = 200 m from edge.

studies almost never include surveys of the predator community in the study area or index predator abundance (Yahner 1996). We indexed small mammal abundance; the overall abundance and distribution of small mammals at forest edge and interior were similar, as were the distributions of depredated ground and shrub nests, but the abundance of small mammals was not related to nest predation for either nest type or location in one season. Either the small mammals that we detected were not major nest predators, or they did not vary sufficiently in abundance in a homogeneous landscape in one season to show a relationship with nest predation. A relationship between nest predation and small mammal abundance may be detectable only over time; small mammals vary greatly from year to year with food abundance (Elkinton et al. 1996). Long-term studies are needed to determine if this is the case.

Small-mouthed nest predators such as *Peromyscus* were abundant in our study area (10–40/ha; Elkinton et al. 1996) compared to larger generalist predators such as fishers (*Martes pennanti*; 21/100 km^2 in central Massachusetts; York 1996) that have been shown to depredate artificial nests in northern New England (DeGraaf 1995). If small eggs that are susceptible to depredation by all potential predators are used in artificial nests, then ubiquitous, abundant predators (e.g., small mammals) may swamp the effect of larger generalist predators, even if the latter are more abundant along forest edges (apparently not the case in the northeastern U.S.). Moreover, our data suggest that ground nests may be particularly vulnerable to predators such as mice and chipmunks (Haskell 1995, Bayne et al. 1997), which spend more time foraging on the ground than in shrubs or trees (Madison 1977, Elliot 1978, Graves et al. 1988). Hence, the hypothesis that egg predation rates are elevated at forest edges may, in large part, be an artifact of egg size. Virtually all studies to date have used quail eggs (see Paton 1994, Major and Kendal 1996; but see George 1987) which apparently cannot be opened by the most abundant small-mouthed predators in temperate forests.

Do natural nests containing small eggs show edge related predation in the extensively forested northeastern U.S.? In a 2-year study of ground nesting Ovenbird (*Seiurus aurocapillus*) reproductive success in New Hampshire (King et al. 1996), nests, territories, and territorial males were equally distributed in edge (0–200 m) and forest interior (201–400 m); nest survival was higher in the forest interior in year 1, but not in year 2. The proportion of pairs fledging at least 1 young, fledgling weight, and fledgling wing chord did not differ between edge and interior over the course of the study.

In extensive mixed-wood forests in New England, edge related differences in artificial nest predation rates have not been consistently demonstrated. In our study predation rates were substantially higher on artificial ground nests that contained small eggs than those in studies that used quail eggs (Table 3). All potential predators can open small eggs, and their use should result in higher predation rates because small-mouthed predators are

more abundant than large nest predators. Predation rates of artificial nests often have been assumed to track those of natural nests (Major and Kendal 1996), but they may not unless egg sizes closely approximate those of the species of concern. For example, nest survival of natural nests was lower than that of experimental nests containing quail eggs in Panama because of the abundance of small-mouthed nest predators (Roper 1992). Predation rates in quail egg experiments (e.g., Loiselle and Hoppes 1983; Martin 1987, 1988) may be useful to compare local habitats, but may be inappropriate for estimating natural predation rates or for comparing areas inhabited by different predators (Roper 1992). Nest predation is a dominant factor in avian reproductive success (Ricklefs 1969, Martin 1988); results of experiments that exclude major sources of mortality (i.e., small-mouthed predators) may not be representative (Roper 1992).

Only if appropriate egg sizes are used can predation rates in relation to habitat edge or placement be generalized or approximated for natural nests. Even then, effects such as nest defense and appearance (Martin 1987) are difficult to address. Our data suggest that egg predation rates may be strongly related to egg size, other factors being equal, because the most abundant predators can only open small eggs.

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BIRD USE OF BURNED AND UNBURNED CONIFEROUS FORESTS DURING WINTER

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ABSTRACT.—Cavity-nesting bird species have been shown to be associated with early post-fire habitat during the breeding season but little study has been done of birds in the non-breeding season. We compared bird composition and foraging behavior during the winter in burned and unburned forests. We conducted point counts during four consecutive winters immediately following a stand replacement fire. Burned and unburned forests had similar numbers of bird species, yet species composition was distinctly different. Trunk and branch foraging species were 2.5 times more abundant in burned forest than in unburned forest. Within burned forests, trunk and branch foraging species significantly decreased from the first winter post-fire to the fourth winter post-fire. We conducted foraging observations of four woodpecker species within burned forests only. Woodpeckers used western larch (*Larix occidentalis*), ponderosa pine (*Pinus ponderosa*) and Douglas-fir (*Pseudotsuga menziesii*) snags that were greater than 23 cm in diameter. Stand replacement fires may play an important role in maintaining populations of trunk and branch foraging species in mixed coniferous forests in northeastern Washington. *Received 24 August 1998, accepted 28 Dec. 1998.*

Wildfire plays a major role in determining landscape patterns by creating large mosaics of burned habitat intermixed with unburned habitat. Prior to fire suppression policies in the early 1900s, wildfires were more frequent and widespread in the western United States (Agee 1994, Hejl 1994). Mixed-conifer forests of the Pacific Northwest have a history of stand replacement fires, in which most trees are killed, occurring every 140–340 years (Agee 1994). Stand replacement fires create a unique habitat of large patches of standing dead trees that host great numbers of bark and wood-boring beetles (Furniss 1965, Amman and Ryan 1991) which serve as food for birds inhabiting recently burned forests (Spring 1965, Wickman 1965). This food resource is thought to decrease dramatically 2–5 years post-fire (Koplin 1972).

Cavity-nesting bird species are associated with early post-fire forests (1–9 years post-fire, Hutto 1995). Many researchers have compared bird abundance in burned and unburned forest during the breeding season and found increased numbers of cavity-nesting bird species in early post-fire forests (Bock and Lynch 1970, Raphael and White 1984, Raphael et al. 1987, Hutto 1995, Caton 1996, Hitchcox 1996). Some species, including the Black-backed Woodpecker (*Picoides arcticus*), Three-toed Woodpecker (*Picoides tridactylus*), and Mountain Bluebird (*Sialia mexicana*) have been shown to be more common in the first few years after a fire than later (Hutto 1995). How long this high abundance of cavity-nesting bird species persists in post-fire habitat is unclear.

There are few data on bird species composition of burned forests during the non-breeding season. In Montana, Blackford (1955) anecdotally noted numerous woodpecker species in burned forests during the winter. Blake (1982) compared stand replacement burned and unburned ponderosa pine (*Pinus ponderosa*) forests during the non-breeding season and found bark insectivores (including woodpeckers) to be more abundant in burned forests. Non-breeding season habitat may play a significant role in determining overall survival and numbers of individuals that breed (Conner 1979, Graber and Graber 1983, Klein 1988) and is probably as important as breeding season habitat for the persistence of avian populations. Many resident species present in burned forest during the non-breeding season may not remain in burned forest year-round but seasonally migrate short distances to different habitats, thereby maximizing their use of available resources.

Several studies have examined the characteristics of trees used for nesting by cavity-nesting birds in burned forests. In general, cavity-nesters seem to prefer broken top snags

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and snags greater than 23 cm in diameter for nesting (Raphael and White 1984, Hutto 1995, Caton 1996, Hitchcox 1996). Fewer researchers have examined the snag characteristics used for foraging by cavity-nesting birds in burned forests (Hutto 1995, Caton 1996), even though food availability may be as important to excavating cavity-nesting species as the availability of nest sites, especially in burned forests where nest snags may be abundant (Caton 1996). Because snags used for nesting and foraging by cavity-nesting birds may differ, information on the characteristics of snags used for nesting would be of particular interest to managers to maintain fire-dependent bird populations.

To investigate the use of burned forests during the winter, we examined bird community composition and foraging behaviors in burned and unburned forests during four consecutive winters in northeastern Washington.

STUDY AREA AND METHODS

Study area.—The study sites were located in the Kettle River Range on the Colville National Forest in the northeastern corner of Washington, 26 km north of Republic (48° 65′ N, 118° 73′ W). This area is predominantly a mixed-conifer forest consisting of subalpine fir (*Abies lasiocarpa*), Douglas-fir (*Pseudotsuga menziesii*), Engelmann spruce (*Picea engelmannii*), ponderosa pine, western larch (*Larix occidentalis*), and lodgepole pine (*Pinus contorta*), with a minor understory component of ninebark (*Physocarpus malvaceus*). Both the burned and unburned study sites had similar tree species composition and were located in unlogged areas.

In August 1994 the Copper Butte fire was ignited by lightning and burned 4000 ha, resulting in large mosaics of high intensity burned areas mixed with low intensity and unburned areas (U.S. Dept. of Agric. 1995). We chose two stand replacement burned sites of greater than 80 ha within the Copper Butte fire area, with elevations ranging from 1320–1650 m. The unburned site was located 20 km north of the burned sites, 0.6 km from the burn boundary. The 80 ha unburned site had similar slope and aspect to the burned sites but was only 1030–1320 m in elevation. Average yearly rainfall for this area is 384 cm and average yearly temperature is 6.1° C. During November–February, when all of the data were collected, the average monthly precipitation was 42 cm (predominantly snow) and the average temperature was −2.1° C.

Avian sampling.—We used the point count method to quantify birds in burned and unburned forests (Blondel et al. 1981, Hutto et al. 1986). Point count stations were systematically laid out at least 200 m apart, 100 m from a change in habitat, and 50 m from roads and creeks. We conducted ten-minute counts, recording all birds seen and heard within 100 m (Hutto 1995). Unfortunately, we could not always distinguish between Hairy (*P. villosus*), Three-toed (*P. tridactylus*), or Black-backed (*P. arcticus*) woodpeckers so we created a category of "unknown woodpecker" to account for these detections. Counts were conducted on fair weather days when winds were less than 25 kph, with little or no precipitation, and temperatures greater than −9° C. Winter counts were conducted between 08:00 PST (1 h after sunrise) and 16:00 from 8 November to 4 February 1994–1997.

Over the four years of the study, the number of point count stations surveyed was as follows: first winter to fourth winter post-fire, burned (8, 9, 13, 13) and unburned (0, 9, 9, 9). The number of stations on the burned site varied over the four years because of logging that occurred in 1996 at four of the stations. These four stations were no longer used, and eight new stations were added in a nearby similarly burned area. The difference in the number of count stations in burned and unburned forest affected bird diversity very little. The four point count stations in addition to nine on the burned study site added only one bird species that was not detected in the first nine stations. On both study sites there were two visits to each point count station during a winter and these were averaged. We used the mean number of birds per point in comparing burned and unburned forests and number of points as sample size.

Bird species were assigned to three foraging guilds based on Ehrlich and coworkers (1988) and Hutto (1995): (1) trunk and branch foragers (timber drillers and timber gleaners), (2) foliage foragers (including aerial foragers), and (3) ground foragers.

Foraging sampling.—We recorded foraging observations of four woodpecker species in the burned forest only, during and after point count surveys. A bird was considered foraging when it appeared to be actively searching for and/or obtaining food (i.e., digging or pecking). Only the first foraging observation was recorded for each individual (Hejl et al. 1990). The following foraging data were recorded: bird species, maneuver (pecking = tapping on the surface, flaking = removing bark, drilling = excavating into wood), zone of foraging (lower trunk, middle trunk, upper trunk, branches), tree species, tree dbh class (8–22, 23–37, 38–53, >53 cm), burn severity of trees (alive and green, possibly alive with some green present, dead with brown needles present, dead and severely burned), and top condition (broken, crooked, double, intact). We combined the foraging data for each species over four winters in order to increase sample size (Morrison 1984). Consequently, we do not have information on between year differences in foraging.

Tree sampling.—Several tree characteristics within the burned forest were recorded at count stations and between stations in 0.04-ha circular samples for a total of 24 samples (Martin 1994): tree species, tree dbh, burn severity, bark cover, branch condition, and top condition.

TABLE 1. Species detected in burned and unburned early post-fire mixed-conifer forests in northeast Washington during the winters, 1994–1997.

Species	Forage guild[a]	Nest guild[b]	Burned[c]		Unburned[c]		P[d]
			Year	Mean/pt	Year	Mean/pt	
Blue Grouse, *Dendragapus obscurus*	G	O	2	0.083	—	0	>0.05
Downy Woodpecker, *Picoides pubescens*	T	C	1,2,4	0.175	—	0	>0.05
Hairy Woodpecker, *Picoides villosus*	T	C	1,2,3,4	0.410	2,4	0.056	0.035
Three-toed Woodpecker, *Picoides tridactylus*	T	C	1,2	0.042	—	0	0.047
Black-backed Woodpecker, *Picoides arcticus*	T	C	1,2,3,4	0.406	2	0.019	0.001
Pileated Woodpecker, *Drycocopus pileatus*	T	C	—	0	3	0.019	>0.05
Unknown Woodpecker	T	C	1,2	0.144	2	0.019	0.05
Gray Jay, *Perisorius canadensis*	F	O	1,2	0.075	2,3	0.093	>0.05
Steller's Jay, *Cyanocitta stelleri*	F	O	—	0	4	0.019	>0.05
Clark's Nutcracker, *Nucifraga columbiana*	F	O	1,2	0.016	—	0	>0.05
Black-billed Magpie, *Pica pica*	G	O	2	0.014	—	0	>0.05
Common Raven, *Corvus corax*	G	O	1	0.016	4	0.037	>0.05
Black-capped Chickadee, *Parus atricapillus*	F	C	1,2	0.031	2	0.074	>0.05
Mountain Chickadee, *Parus gambeli*	F	C	1,2,3,4	0.179	2,3,4	0.352	>0.05
White-breasted Nuthatch, *Sitta carolinensis*	T	C	4	0.048	—	0	>0.05
Red-breasted Nuthatch, *Sitta canadensis*	T	C	—	0	2,3,4	0.389	0.001
Brown Creeper, *Certhis americana*	T	C	3	0.019	—	0	>0.05
Winter Wren, *Troglodytes troglodytes*	G	O	—	0	4	0.019	>0.05
Golden-crowned Kinglet, *Regulus satrapa*	F	O	—	0	2,3,4	0.260	0.001
Varied Thrush, *Ixoreus naevius*	G	O	—	0	4	0.056	>0.05
Red Crossbill, *Loxia curvirostra*	F	O	2,4	0.067	2	0.148	>0.05

[a] Forage guild: T = trunk and branch, F = foliage, G = ground.
[b] Nest guild: O = open, C = cavity.
[c] Burned and Unburned: year: year post-fire that bird species were present during the winter, mean/pt: mean number of birds per point averaged over 4 years.
[d] P-value: 2-way ANOVA, treatment effect (burned-unburned).

Statistical analyses.—The mean numbers of birds per point in burned and unburned forests were compared with a 2-way Analysis of Variance (ANOVA). Bird abundance between years within a treatment was compared using a Kruskal-Wallis nonparametric 1-way ANOVA and pairwise comparisons were made using Tukey's HSD procedure. Bird abundances, grouped by foraging guilds, were compared between burned and unburned forests using a Mann-Whitney U-test. To determine trends in abundance over four years, a Spearman rank order correlation was performed (Zar 1996). Comparisons of foraging observations and available vegetation were made using the χ^2 Goodness of Fit test for categorical data. For example, if the distribution of tree species used by Downy Woodpeckers was significantly different than the proportion of available tree species the Goodness of Fit test would have a $P < 0.05$. P values of less than 0.05 were considered significant for all tests. Statistical analyses were performed using SPSS (SPSS 1993).

RESULTS

Winter bird assemblage in burned and unburned forests.—During the winter, 20 bird species were detected in burned and unburned forests combined (Table 1). Bird species composition differed between the two forests. In burned forests 7 of the 14 species detected were restricted to burned forests and in unburned forests, 6 of the 14 species detected were restricted to unburned forests. Averaged over four years trunk and branch foraging species were 2.5 times more abundant in burned forest ($U = 2.0$, df = 1, $P > 0.05$), and foliage foraging species were 3 times more abundant in unburned forest ($U = 2.0$, df = 1, $P > 0.05$; Fig. 1). Woodpecker species combined were 10 times more abundant in burned forests than in unburned forest. The four most abundant species detected in burned forest in descending order were the Hairy Woodpecker, Black-backed Woodpecker, Mountain Chickadee (*Parus gambeli*), and Downy Woodpecker (*Picoides pubescens*), and in unburned forest the Red-breasted Nuthatch (*Sitta canadensis*), Mountain Chickadee, Golden-crowned Kinglet (*Regulus satrapa*), and Red Crossbill (*Loxia curvirostra*). Black-backed Woodpeckers (2-way ANOVA: $F = 11.26$, df = 1, $P = 0.001$) and Hairy Woodpeckers ($F = 4.62$, df = 1, $P = 0.035$) were significantly more abun-

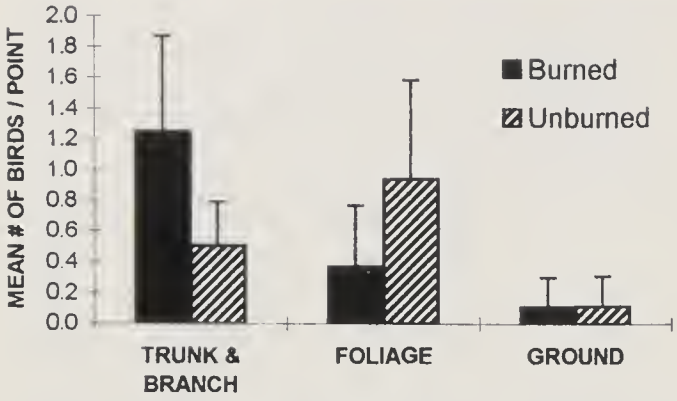

FIG. 1. Mean (±SD) number of birds per point over four years, by foraging guild in burned and unburned forests during winter (Mann-Whitney *U*-test: for each guild all $P > 0.05$).

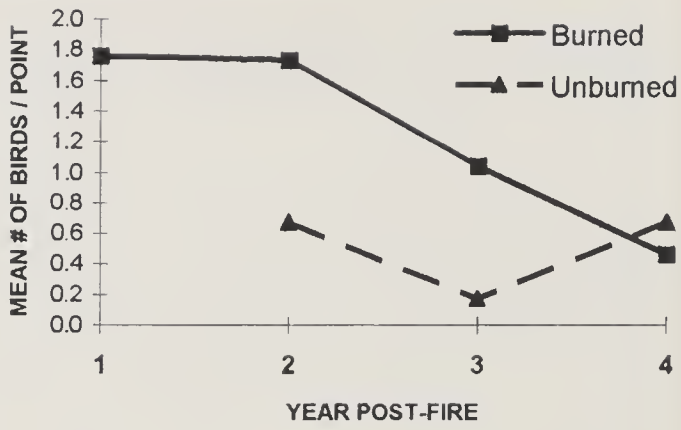

FIG. 2. Trunk and branch foraging species abundance over four years, in burned and unburned forest during winter (Spearman rank: Burned $s_r = -1.0$, df = 3, $P = 0.001$; Unburned $s_r = 0$, df = 2, $P > 0.05$).

dant in burned forest regardless of year (Table 1). The Three-toed Woodpecker was significantly more abundant ($F = 4.12$, df = 1, $P = 0.047$) in burned forest only during the second winter post-fire (Kruskal-Wallis: $\chi^2 = 11.9$, df = 3, $P = 0.008$; Tukey $P = 0.042$). The Red-breasted Nuthatch ($F = 13.10$, df = 1, $P = 0.001$) and Golden-crowned Kinglet ($F = 11.80$, df = 1, $P = 0.001$) were significantly more abundant in unburned forest.

Change in bird abundance over four years.—Bird species composition and abundance in burned forests during the winter changed from 1994–1997. Eleven species were present the first or second winter post-fire and were absent by the third winter post-fire (Table 1). The Brown Creeper (*Certhia americana*) was not present until the third winter post-fire and the White-breasted Nuthatch (*Sitta canadensis*) was not present until the fourth winter post-fire. The abundance of trunk and branch foraging species decreased 3.8 times from winter 1994–1997 and showed a significant negative trend (Spearman rank: $r_s = -1.0$, $P = 0.001$; Fig. 2). Although all four woodpecker species present in burned forest during the winter had declined by the fourth winter post-fire, none of the changes was significant (all $P > 0.05$). Within burned forest there was no significant trend in the abundance of foliage and ground foraging species from 1994–1997. Within unburned forest there was a significant decreasing trend of foliage foraging species ($r_s = -1.0$, $P = 0.001$) during the four years.

Foraging.—In burned forest Downy, Hairy, Three-toed, and Black-backed woodpeckers foraged upon standing dead trees 99% of the time and 1% of the time on logs ($n = 145$). Woodpeckers used burned trees with brown needles 51% of the time, significantly different than the proportion available (20%; Goodness of Fit: $\chi^2 = 14.98$, df = 2, $P = 0.001$). They foraged predominantly on Douglas-fir (61%), western larch (38%), and ponderosa pine (38%; Fig. 3). Western larch (13% available) and ponderosa pine (2% available) were used for foraging significantly more than expected ($\chi^2 = 60.58$, df = 4, $P = 0.001$). Trees greater than 23 cm in diameter were used (84%) significantly more than the proportion available (36%; Fig. 4; $\chi^2 = 85.86$, df = 3, $P = 0.001$). Broken top snags were used (14%) in similar proportions to their availability (12%; $\chi^2 = 0.28$, df = 1, $P > 0.05$). Available snags consisted mainly of severely burned (80%), intact top (83%), Douglas-fir (78%), western larch (13%), or sub-alpine fir (6%) with a mean diameter of 22 cm.

The four woodpecker species foraged differently. Downy Woodpeckers foraged predominantly by pecking while Hairy, Three-toed, and Black-backed woodpeckers foraged predominantly by flaking and drilling. Hairy and Three-toed woodpeckers foraged on similar tree species (Fig. 3) and on similar parts of trees (Fig. 5). Black-backed Woodpeckers foraged on western larch and Douglas-fir (Fig. 3) and foraged predominantly on the middle and lower trunks, of trees (Fig. 5). Downy Woodpeckers foraged most frequently on branches of ponderosa pine (Figs. 3, 5).

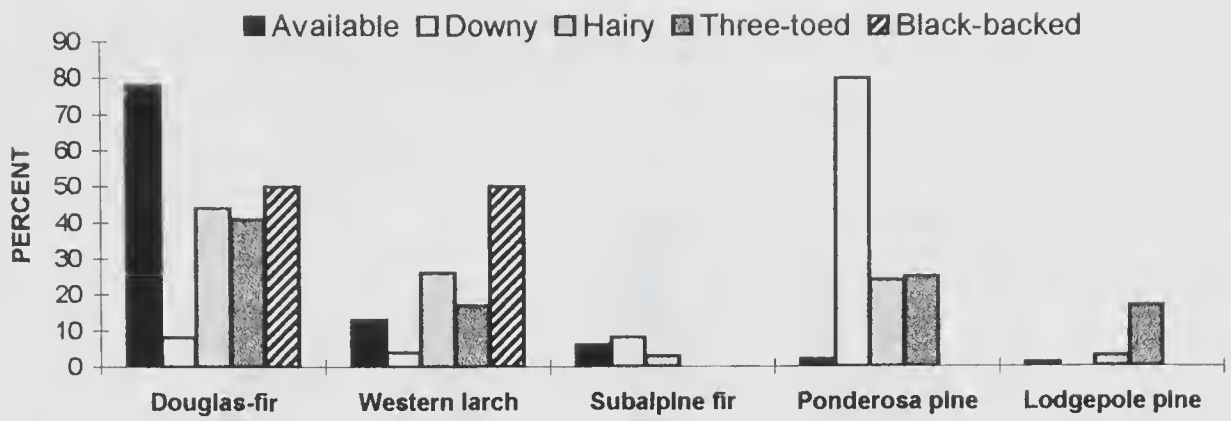

FIG. 3. Proportion of tree species available and used for foraging by four woodpecker species during winter in burned forests (Goodness of Fit, the tree species distribution used by all woodpeckers combined was significantly different than the available distribution, $\chi^2 = 60.58$, df = 4, $P = 0.001$; each bird species used a significantly different tree species distribution than what was available (all $P < 0.001$) and each bird species foraged on different tree species than each other (all $P < 0.003$) except Hairy and Three-toed woodpeckers which foraged similarly ($\chi^2 = 3.573$, df = 4, $P > 0.05$)).

DISCUSSION

Trunk and branch foraging species were more abundant in recently burned forests than in unburned forests. Other studies of burned forests had similar results (Raphael and White 1984, Hutto 1995). This may be due to changes in forest structure and related food resources as a result of stand replacement fire. Stand replacement fire changes the structure of a forest from a dense canopy cover, with shrub undergrowth and few standing dead trees to little canopy cover, few shrubs, and numerous standing dead trees. Food in unburned forests include a variety of seeds and insects on foliage, bark, and shrubs. During the winter, food in burned forests may be limited to seeds from fire opened cones and bark and wood-boring beetle larvae in fire-killed trees (Hutto 1995). Bird species that forage on the ground and foliage probably have more food available in unburned forests, and species that forage on trunks and branches of trees probably have more food available in burned forests. Bark and wood-boring beetle larvae that are abundant in fire-killed trees are the major food source of woodpeckers, especially during winter (Brawn et al. 1982). Therefore, fire-killed trees may be crucial in supplying year round food for trunk and branch foraging species. Large diameter, thick barked snags are typical locations for bark and wood-boring beetle larvae (Otvos 1965). Woodpecker species in this

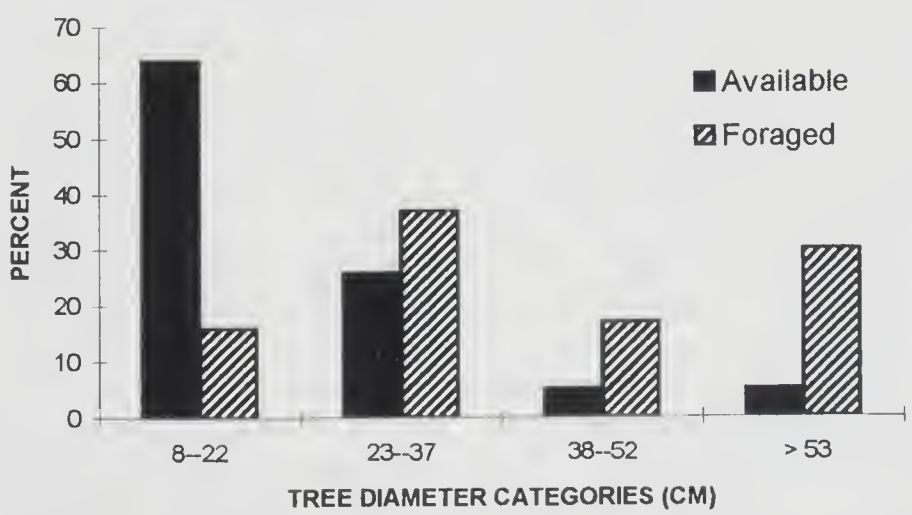

FIG. 4. Proportion of tree diameters available ($n = 173$) and used for foraging ($n = 145$) by woodpeckers in burned forests. Significantly different tree diameters were used than what was available (Goodness of Fit, $\chi^2 = 85.86$, df = 3, $P = 0.001$).

FIG. 5. Foraging zones used by four woodpecker species during winter in burned forests [Goodness of Fit: Downy (n = 26, χ^2 = 20.89, df = 3, P = 0.001) and Black-backed (n = 42, χ^2 = 14.83, df = 3, P = 0.002) woodpeckers used zones significantly different from an even distribution. Each woodpecker species foraged in significantly different zones from each other (all $P < 0.012$) except Hairy (n = 55) and Three-toed (n = 12) woodpeckers which foraged in similar zones (χ^2 = 6.01, df = 3, $P > 0.05$)].

study used large snags between 23 and 37 cm dbh disproportionately more often for foraging in burned forest. In Montana, the average foraging snag diameter was 10–30 cm (Caton 1996). Snag species used most often for foraging in this study included thick barked western larch, ponderosa pine, and Douglas-fir. Hutto (1995) and Caton (1996) also found that woodpeckers foraged on these same snag species in burned forests in Montana.

Within burned forest there were several changes in the bird community from the first winter post-fire to the fourth. Some species were present only the first or second winter and were absent by the third winter. Woodpeckers, however, decreased in abundance from the first winter to levels equal to that found in unburned forests by the fourth winter. In the Sierra Nevada Mountains, Bock and Lynch (1970) found woodpeckers to be in low numbers by six years post-fire. Hutto (1995) found Three-toed and Black-backed woodpeckers to be most common 1–9 years post-fire. Post-fire forests appear to support a succession of bird species, with early post-fire conditions being conducive to specific woodpecker species. The decrease in abundance of the Downy, Hairy, Three-toed, and Black-backed woodpeckers may have occurred as a result of a decrease in food resources. Bark and wood-boring beetle larvae dramatically decrease 2–5 years post-fire (Koplin 1972). Food resources may be as important to the distribution of these species as nest-site availability. Caton (1996) suggested that the availability of suitable foraging snags played a large role in the distribution of woodpecker species in burned forests in Montana. Further studies on food resource availability in burned and unburned forests may better help explain their distribution.

Non-breeding season habitat quality is probably as important to the persistence of bird populations as breeding season habitat (Conner 1979) because most bird mortality occurs during the non-breeding season (Graber and Graber 1983). Favorable winter habitat can increase winter survival and result in more birds breeding the following season. Local movements to burned habitats by resident bird species may increase survival. The use of burned forests during the winter by woodpeckers may also increase their overwinter survivorship by increasing food and decreasing predation. Different foraging techniques observed by woodpeckers in burned forest may allow many species to coexist. All of these factors may contribute to the increased capability of recently burned forests to support bird species, including woodpeckers, during the non-breeding season.

The 100 m radius point counts seemed to be an adequate way to compare the relative abundance of birds in these two forests. Visual detections of birds in the burned and unburned forests were probably different, and audible detections, which most of ours were, were probably similar in the two forests. Differenc-

es in auditory detections were most likely minimal during the winter when it was extremely quiet. Dellasala and coworkers (1996) found little difference in detection rates of birds in 100 m radius point counts in young (20 yr) and old growth forests.

Fire suppression over the past 100 years (Agee 1994, Hejl 1994) has probably had a major effect on bird communities in mixed-conifer forests. Stand replacement fires may help to increase populations of cavity-nesting and trunk and branch foraging species. Populations of Hairy, Three-toed, and Black-backed woodpeckers might be maintained by periodic occurrences of stand replacement fires throughout the landscape. The spatial and temporal pattern of stand replacement fires needed to maintain bird populations needs further investigation.

Management implications.—Forest managers can increase cavity-nesting bird populations by relaxing fire suppression policies and/or by initiating prescribed burning programs. To manage for cavity-nesting birds in burned forests snags of western larch, ponderosa pine and Douglas-fir larger than 23 cm in diameter should be present. If managers can delay logging of burned forests three to four years, the habitat will be less suitable for trunk and branch foraging species and logging may have less impact on these species. Future studies investigating snag densities and patch sizes of burned forests required to maintain populations of cavity-nesting species during summer and winter are needed to help managers provide for these species.

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NEST PREDATORS OF OPEN AND CAVITY NESTING BIRDS IN OAK WOODLANDS

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ABSTRACT.—Camera setups revealed at least three species of rodents and seven species of birds as potential predators at artificial open nests. Surprisingly, among avian predators identified at open nests, one third were Bullock's Orioles (*Icterus bullockii*). Two rodent species and three bird species were potential predators at artificial cavity nests. This high predator diversity was consistent with previous studies, although the number of avian predators at open nests was higher than expected. *Received 31 March 1998, accepted 22 Nov. 1998.*

As the primary source of nest failure among birds (Lack 1968, Ricklefs 1969), predation is a likely factor affecting species' coexistence, habitat selection, and conservation (Zimmerman 1984; Martin 1988a, b). When nest predation differs among species, habitats, and locations, it can influence life history traits such as clutch size, nest placement, developmental period, and number of broods (Ricklefs 1969; Martin 1988c, 1995). Avian ecologists generally agree that predation rates differ among species nesting in cavities and open (cup) nests (Lack 1954, Nice 1957, Ricklefs 1969). Predators may differ as well, but little is known about predators of bird nests because predation is rarely observed, and observations are biased toward diurnal predators. Some researchers have made assumptions about broad classes of predators based on the appearance of the depredated nest, but few data exist to support those assumptions, and authors disagree on evidence used to assign depredated nests to predator groups and the reliability of the evidence (Best 1978, Best and Stauffer 1980, Wray et al. 1982, Boag et al. 1984, Hernandez et al. 1998a, Marini and Melo 1998). Here we report results of a camera study at both artificial open and cavity nests. The primary objective of our study was to identify nest predators as part of a larger study of reproductive success among birds in oak-pine woodlands in the west-central foothills of the Sierra Nevada of California.

STUDY AREA AND METHODS

The study was done at the San Joaquin Experimental Range, approximately 40 km north of Fresno, California. The San Joaquin Experimental Range covers about 1875 ha and ranges in elevation from 215 to 520 m. Climate is Mediterranean, with cool, wet winters and hot, dry summers. A sparse woodland overstory of blue oak (*Quercus douglasii*), interior live oak (*Q. wislizenii*), and foothill pine (*Pinus sabiniana*) covers most of the San Joaquin Experimental Range. A scattered understory of shrubs includes mainly wedgeleaf ceanothus (*Ceanothus cuneatus*), chaparral whitethorn (*C. leucodermis*), redberry (*Rhamnus crocea*), and mariposa manzanita (*Arctostaphylos viscida mariposa*). The San Joaquin Experimental Range has been lightly to moderately grazed since about 1900 and is surrounded on all sides by similar habitat.

Using nests of California Towhees (*Pipilo crissalis*) collected at the end of the previous field season, we situated artificial open nests low in small trees or shrubs in positions similar to those known to be used by California Towhees (on a forked branch or supported by several twigs). At cavity setups, eggs were placed with a "pick-up" tool, using cavities known to be deep enough for cavity-nesting species at the San Joaquin Experimental Range. Most cavities were excavated by primary cavity nesters, but some natural cavities previously used for nesting were also used. A fiberscope (Purcell 1997) was used to guide the placement of eggs in cavities, to monitor eggs for possible predation, and to measure cavity depth. To avoid leaving olfactory cues at nests, field personnel washed their hands before going into the field with a soap developed to remove human scent and sprayed their boots with a scent masker. We avoided dead-end trails and did not create paths that might lead predators to nests.

One experimental egg was placed in open nests, and one or two eggs were placed in cavity nests, the number and type depending on availability. Most eggs used in open nests were from wild House Sparrows (*Passer domesticus*) or captive Ringed Turtle-Doves (*Streptopelia risoria*); most eggs in cavities were from captive Zebra Finches (*Poephila gullata*). We sometimes used a Buttonquail (*Turnix* sp.) egg as the second egg in a cavity nest. House Sparrow eggs were slightly smaller and Ringed Turtle-dove eggs slightly larger than those of California Towhees (see Baicich and Harrison 1997). Although similar in size to eggs of the Plain Titmouse (*Baeolophus inornatus*), the Zebra Finch

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eggs were smaller than eggs of all cavity-nesting species in our study area.

Predation at open nests was monitored mechanically, with an egg encircled by a loop of wire attached within a nest of the California Towhee. Removal of the egg activated an electrieal signal to a solenoid, tripping a camera mounted nearby. We used inexpensive, autofocus, autoflash, Keystone 550D or 590AF cameras, allowing identification of both diurnal and noeturnal predators. (Trade names and commercial products are mentioned for information only; no endorsement by the U.S. Department of Agriculture is implied.) Details on the mechanieal system for open nests are available from KLP. At eavity nests, we used Trailmaster Active Infrared trail monitors with weatherproof, autoflash 35 mm eameras to monitor predation. One box that transmitted (12.1 cm L × 8.3 cm W × 4.6 em D) and one that received (19.1 cm L × 8.9 cm W × 5.3 cm D) the infrared beam were placed on each side of the cavity so that an animal entering it would break the beam, triggering the camera positioned on a nearby branch with a good view of the cavity. Beeause Trailmaster units are designed to be set up horizontally aeross trails, we modified the boxes so they could be attached easily to the tree bole or limb with bungee cords. Sensitivity was set at the minimum delay of 0.5 s (one pulse) before an event was reeorded, and the camera delay between photos was set at the minimum of 6 s.

Based on the nesting seasons of eavity- and open-nesting speeies, eameras were set up from March through Junc 1995 (eavities) and April through June 1995 (open). We used 10 open-nest setups to monitor 70 open nests, and 7 Trailmaster monitors at 61 eavity nests. Some data on eavity nests were also ineluded from the 1993 and 1994 field seasons (eight eaeh year). All setups were ehecked about every 4 days. If an egg was taken, or not taken after 14 days, the setup was dismantled and moved to another loeation and installed using fresh eggs.

All artificial nests of the same nest type were separated by at least 200 m in an effort to reduee the chance of visitation by the same animal at two or more setups. This distanee was thought to be enough to assure independent samplcs of the small mammals identified as predators in this study. Based on spot mapping at the San Joaquin Experimental Range (unpublished data), territories of the Western Scrub-Jay (*Aphelocoma californica*), a common nest predator, were approximately 120–210 m in diameter. Mean territory diameters of other common bird species ranged from 180 m (California Towhee) to 310 m (Western Kingbird, *Tyrannus verticalis*). Some eavity setups were eloser than 200 m to open set-ups, but eameras and eggs were not placed concurrently at the two nest types.

At open nests, we measured nest height and the height and diameter of the shrub or small tree containing the nest. Diameter was measured as the mean of the maximum crown diameter and the widest diameter perpendicular to the maximum diameter. At cavity nests, we measured nest height, eavity depth, and horizontal and vertical entrance diameters. We tested differences in these attributes between predated and unpredated nests using two-tailed *t*-tests (SAS version 6.12 for Windows, SAS Institute 1988), $\alpha = 0.05$, and Bonferroni adjustments for multiple tests. We calculated power according to Abramowitz and Stegun (1964) based on specified effeet sizes, an α of 0.05, and two-tailed tests using an inhouse SAS program.

RESULTS

Open nests.—Eggs were removed from 39 of the 70 open nest setups, but we could identify the animals at only 29 of those. Rodents were identified at four (14%): deer mouse (*Peromyscus* spp., two cases), California ground squirrel (*Spermophilus beecheyi,* one case), and Merriam's chipmunk (*Eutamias merriami,* one case). At least five bird species were photographed at the remaining 25 nests (86%) from which an egg was taken: Western Scrub-Jay (12 cases), Bullock's Oriole (*Icterus bullockii,* 7 cases), Acorn Woodpecker (*Melanerpes formicivorus,* 1 case), Western Kingbird (1 case, a pair), and California Towhee (1 case). We could not identify the bird species at the three remaining setups.

In three additional cases, eggs were pecked, chewed, or otherwise damaged but not removed. A pair of Plain Titmice pecked a large hole in the egg at one nest; a female Brown-headed Cowbird (*Molothrus ater*) punctured the egg in another nest; and either a dusky-footed woodrat (*Neotoma fuscipes*) or a Western Scrub-Jay chewed or pecked another egg (both species were photographed).

We may have underestimated nocturnal predation. Only one photo of a deer mouse was taken at night. In 2 of the 10 cases with no identifiable predator, photos were taken at night but were dark, perhaps because the camera's flash was too far from the nest or failed to operate properly (see also Hernandez et al. 1998b).

No attribute measured at open nest setups differed significantly between predated and nonpredated nests (Table 1; $P > 0.05$ in all cases, $P < 0.017$ required for Bonferroni adjustment for multiple tests).

Cavity nests.—Photos were taken at 47 of 69 cavity nests where the egg was removed or pecked open. Interpretation of the photos was complicated, however. First, the minimum camera delay did not allow a photo each

TABLE 1. Nest site variables and results of *t*-tests for nonpredated (n = 18) and predated (n = 48) open nests at the San Joaquin Experimental Range.

	Nonpredated open nests Mean (SE)	Predated open nests Mean (SE)	P[a]	Power
Nest height (m)	1.21 (0.11)	1.11 (0.06)	0.48	0.97[b]
Substrate height (m)	4.61 (0.81)	4.25 (0.41)	0.67	0.91[c]
Substrate diameter (m)	6.03 (1.34)	4.90 (0.40)	0.43	0.82[c]

[a] A P-value of 0.017 is needed for significance at $\alpha = 0.05$ after Bonferroni adjustment for multiple comparisons.
[b] Based on an effect size of 0.5m.
[c] Based on an effect size of 3 m.

time the infrared beam was broken after an initial photo was taken. Consequently, photos rarely showed animals leaving a cavity nest and none showed one "caught in the act" of leaving with an egg. We had to assume that an animal in a photo consumed the missing egg. Second, in seven cases the egg was gone and no animal was evident in the photo (see also Brooks 1996). The departure of some predators from a cavity may have been too rapid for it to be caught in the photo, or photos with no animal may have resulted from direct sunlight entering the receiver window (Kucera and Barrett 1993). Third, in 15 instances more than one species entered the cavity and tripped the camera before we found that the egg was gone. Fourth, in 16 cases nest material was added to the cavity by birds or mammals so we could not ascertain whether the eggs had been eaten or simply buried. We did not include these cases in our comparisons of predated and nonpredated nests.

In nine cavity setups with missing eggs, only one species appeared in the photos. The assumed predators were European Starling (*Sturnus vulgaris;* four cases), House Wren (*Troglodytes aedon;* one case), Western Bluebird (*Sialia mexicana*; one case), deer mouse (one case), and unidentified squirrels (probably California ground squirrels; two cases). All photos were taken during daylight hours except that of the deer mouse.

No attribute measured at cavity nests differed significantly between predated and nonpredated nests (Table 2; $P > 0.05$ in all cases, $P < 0.01$ required after adjusting for multiple tests).

DISCUSSION

Our results are consistent with other studies using artificial nests in finding a high diversity of nest predators, ranging from six to nine species (Henry 1969, Wilcove 1985, Reitsma et al. 1990, Leimgruber et al. 1994). We identified eight species at open nests, and two (possibly three) other species pecked or pierced eggs. Picman and Schriml (1994) found only one or two major predator species in each of four vegetation types, although predator diversity ranged from four (marsh) to nine species (scrubland and forest). Lack of independence of the setups in their study may have overestimated the importance of some predator species (see below). Interestingly, all

TABLE 2. Nest site variables and results of *t*-tests for predated and nonpredated cavity nests at the San Joaquin Experimental Range.

	Nonpredated cavities		Predated cavities			
	Mean (SE)	n	Mean (SE)	n	P[a]	Power
Nest height (m)	3.82 (0.24)	35	3.78 (0.23)	32	0.90	0.98[b]
Depth (cm)	25.1 (1.94)	35	31.0 (2.42)	31	0.06	0.95[c]
Vertical entrance diameter (cm)	5.68 (0.67)	34	5.06 (0.16)	30	0.37	1.00[d]
Horizontal entrance diameter (cm)	5.19 (0.19)	34	5.14 (0.13)	30	0.83	0.98[d]
Minimum entrance diameter (cm)	4.80 (0.15)	34	4.94 (0.14)	30	0.51	0.99[d]

[a] A P-value of 0.010 is needed for significance at $\alpha = 0.05$ after Bonferroni adjustment for multiple comparisons.
[b] Based on an effect size of 1 m.
[c] Based on an effect size of 0.5 cm.
[d] Based on an effect size of 1.0 cm.

but one (Acorn Woodpecker) of the avian predators at open nests in our study were open nesters and all avian predators at cavity nests were cavity nesters.

We know of only two efforts to study predation at experimental cavity nests (Wilcove 1985, Sandström 1991), neither of which identified predators. Although some species photographed at our cavity setups may have been only reconnoitering potential nest sites, they may also opportunistically eat eggs thus encountered in a cavity. The importance of birds as predators at active cavity nests, defended by nesting birds, is unknown but probably significant in some instances. European Starlings are known to usurp nest sites from other bird species (Troetschler 1976, Ingold 1989) and, although the contents of the cavities were unknown, eggs were likely present in some when usurpation occurred late enough in the nesting cycle for egg-laying or incubation to have begun. Our results suggest that starlings probably consume eggs in the course of usurping nest sites.

Although several species of corvids are believed to be important predators at open nests (Yahner and Wright 1985, Yahner and Scott 1988, Andrén 1992, Picman and Schriml 1994, Hannon and Cotterill 1998), nest predation at open nests by noncorvids has not often been documented. Gates and Gysel (1978) reported anecdotal evidence of nest predation by an Eastern Screech-Owl (*Otus asio*). Picman (1987) photographed Marsh Wrens (*Cistothorus palustrus*), House Wrens, and Gray Catbirds (*Dumetella carolinensis*) predating nests. Picman and Schriml (1994) recorded predation events by Broad-winged Hawks (*Buteo platypterus*), Eastern Meadowlarks (*Sturnella magna*), and Red-winged Blackbirds (*Agelaius phoeniceus*). The Marsh Wren was the only predator recorded at nests of Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*; Picman and Isabelle 1995). Predation of open nests by woodpeckers has been documented rarely (Bent 1939; Watt 1980; Hernandez et al. 1998a, b; Robert Cooper, unpubl. data), and never by the Acorn Woodpecker. Egg removal by Bullock's Orioles was surprisingly common in this study. Both sexes of this oriole are known to be ejectors of Brown-headed Cowbird eggs, and they sometimes consume the eggs before removing the shells (Sealy and Neudorf 1995). Although some of these "predators" may destroy nests or eggs with no nutritional motivation, predation of open nests by noncorvids may be more frequent than previously thought.

Leimgruber and coworkers (1994) and Picman and Schriml (1994) also found that potential predators visiting nests did not always eat the eggs. Consistent with the findings of Picman and Schriml, mammals in our study nearly always took the egg. Picman and Schriml (1994) classified as "accidental visitors" several bird species that visited nests, including Red-winged Blackbirds, that apparently ate eggs at 6 of 29 nests visited. Regardless of motivation, the effect of egg removal on the nesting birds is the same.

Artificial nest studies are just that—artificial; some biases are certainly involved (Martin 1987, Reitsma et al. 1990, Whelan et al. 1994, Marini and Melo 1998, Wilson et al. 1998). As visual predators, birds may key in on cameras or unrealistic nest placements, or they may follow field workers and learn to associate conspicuous markers at nests with food (Picozzi 1975, Götmark 1992). At open nests we were able to attain a realistic nest placement or a good camera view, but usually not both. At cavity nests, the transmitters and receivers may have inhibited predators from going to a cavity or may have attracted curious predators. Predation also may have been more or less likely at artificial nests than real nests defended by adult birds, but even real nests are left unattended at regular intervals. In spite of these potential biases, we feel that useful data can be obtained from studies of artificial nests because they establish baseline data in an arena where so little is known.

We believe that the value of studies using artificial nests can be substantially increased if studies are designed more carefully to reduce potential biases. For example, most of the studies we reviewed used distances between setups ranging from 20 to 60 m. Such short intervals risk detection of the same individual predator at two or more setups, violating assumptions of independence. Ideally, the distance between artificial nests should exceed the largest home-range diameter of the suite of likely predators. One might argue that shorter distances are appropriate for examin-

ing predation rates, although rates from artificial nest studies are of questionable value for extrapolation to natural conditions (Martin 1987, Whelan et al. 1994, Wilson et al. 1998). Replication over large areas is required to characterize the suite of predators for a given vegetation type, since predators are often unevenly distributed in space and time.

Further problems of independence may have occurred in studies that replaced eggs in nests that had been predated previously. Nour and coworkers (1993) suggested that such egg replacement may not be a problem in studies using plasticine eggs or eggs made from modeling clay because the eggs are not eaten and provide the predator no incentive to return, although predators could avoid nests with clay eggs because of prior negative conditioning.

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Short Communications

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Juvenile Marbled Murrelet Nurseries and the Productivity Index

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ABSTRACT.—Late summer counts of juveniles at sea are used as an index of Marbled Murrelet (*Brachyramphus marmoratus*) reproductive success, but little is known about juvenile dispersal or habitat use. Further, it is not known whether these counts accurately reflect absolute breeding success. To address these questions we conducted five boat surveys for Marbled Murrelets and Pigeon Guillemots (*Cepphus columba*) in Kachemak Bay, Alaska between 7–24 August 1996. Juvenile murrelet distribution in the bay was patchy, and we identified a juvenile Marbled Murrelet 'nursery' area in the outer bay. Fifty-three of 61 juvenile murrelets were in this area, whereas after-hatch-year (AHY) murrelets were dispersed throughout the bay, as were juvenile and AHY Pigeon Guillemots. The murrelet nursery was characterized by water inside of or at the edge of a 20 m deep contour, semi-protected seas, productive waters, and a large bed of *Nereocystis* kelp. Juveniles comprised 16.1% of all murrelets and 24.8% of all guillemots observed at sea. These data suggest a maximum reproductive success of 0.32 chicks/pair if all AHY murrelets were breeding and 0.46 chicks/pair if only 70% of AHY murrelets were breeding. For guillemots, maximum productivity estimated from at-sea counts was 0.50 chicks/pair if all AHY were breeding and 0.71 chicks/pair if only 70% were breeding. The guillemot estimate was similar to that obtained by concurrent studies at nine guillemot colonies in the bay (0.56 chicks/pair). These results suggest that at sea surveys in late summer provide a reasonable index of local productivity for nearshore alcids. Further, if murrelet nursery areas can be found, at sea counts may provide a valid measure of absolute productivity. *Received 11 June 1998, accepted 7 Jan. 1999.*

Nests of the Marbled Murrelet (*Brachyramphus marmoratus*) are difficult to find or study, and reproductive success is known only from widely scattered nests studied over many years. Because of the murrelet's threatened status from British Columbia to California (Ralph et al. 1995), considerable effort has been devoted to finding alternate means of estimating murrelet reproductive success. The most practical approach is to use a productivity index based on surveys at sea, which uses the ratio of juveniles to adults or juvenile densities during the fledging period as indices of production (Ralph and Long 1995, Strong 1995, Kuletz and Kendall 1998). To be accurate, surveys require some knowledge of fledgling dispersal at sea, but little is known about juvenile movements or habitat use.

Anecdotal evidence suggests that juvenile Marbled Murrelets sometimes congregate in "nursery areas", often near shore or in extensive kelp beds (Sealy 1975, Beissinger 1995, Strachan et al. 1995, Strong et al. 1995). If juveniles gather in specific habitats after fledging, productivity surveys could be improved by identifying their location and time of use. Here, we report on a juvenile murrelet nursery and describe associated habitat features. We estimate murrelet productivity from the ratio of juveniles to adults at sea, and compare this with Pigeon Guillemot (*Cepphus columba*) productivity estimates obtained by both counts at sea and local colony studies.

STUDY AREA AND METHODS

We conducted surveys in Kachemak Bay, southcentral Alaska on five days between 7–24 August 1996 (Fig. 1). We surveyed the south side of Kachemak Bay because Marbled Murrelet densities are highest on the south side, which has deep water, many side bays, and a predominantly rocky, convoluted shoreline (Agler et al. 1998).

From a 10 m vessel we counted all Marbled Murrelets and Pigeon Guillemots within 100 m either side of the boat. Two observers used 8 × 42 and 10 × 50 binoculars to identify species and plumages. Juvenile murrelets, which resemble adults in basic plumage, were identified using characteristics described in Carter and Stein (1995) and Kuletz and Kendall (1998). A third person entered observations into a laptop computer using DLOG (Ecological Consulting Inc., Port-

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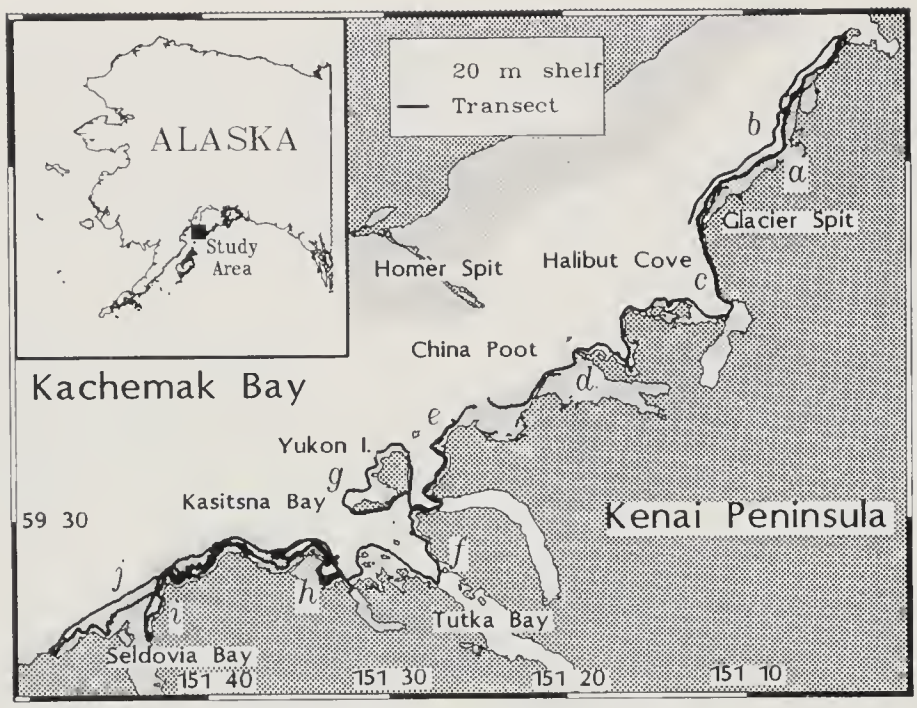

FIG. 1. Survey routes (*a–j*) in Kachemak Bay, Alaska, surveyed by boat on five days on 7–24 August 1996.

land, Oregon). The DLOG data entry program was linked with a Global Positioning System and every observation had an associated latitude and longitude. Survey routes followed a path parallel to shore. For most of the survey we used radar to maintain a distance of 100 m from shore. In rocky or shallow sections we surveyed outside the 20 m depth contour. From the head of the bay to Glacier Spit, and from Kasitsna Bay to Seldovia Bay, we also surveyed 0.5–1.0 km offshore (Fig. 1). The vessel traveled at speeds of about 7 km/hr, but because this was a reconnaissance survey, we temporarily paused or left our path to observe potential juvenile murrelets or guillemots (birds in black and white plumages).

We surveyed a linear distance of 214 km on 10 different survey routes over five days for a total area surveyed of 36.6 km^2 (Table 1). We refer to the area from the head of Kachemak Bay to China Poot Bay as the inner bay and the area west of China Poot to Seldovia Bay as the outer bay. Our main objective was to describe the spatial distribution of murrelets during the fledging period, but we obtained some temporal coverage. Portions of the survey routes overlapped on different days and all regions of the bay were surveyed both early and late in the fledging period (Table 1). Survey dates (7–24 August) encompassed the main and peak fledging period for murrelets, based on five replicate surveys conducted independently between 7 August and 4 September 1996 near Kasitsna Bay by KJK and J. Figurski. These dates correspond to the

TABLE 1. Numbers of adult (after-hatch-year) and juvenile Marbled Murrelets and Pigeon Guillemots observed on survey routes in Kachemak Bay, Alaska, in August 1996. Area (km^2) was calculated from the survey route length × width.

Bay area	Survey route	Date	Area (km^2)	No. Marbled Murrelets		No. Pigeon Guillemots	
				Adults	Juveniles	Adults	Juveniles
Inner	*a*	8–13	2.86	72	0	8	4
Inner	*b*	8–24	3.44	83	1	5	16
Inner	*c*	8–13	3.64	19	0	25	3
Inner	*d*	8–24	1.52	12	1	10	1
Total			11.46	186	2	48	24
Outer	*e*	8–13	2.89	37	1	21	1
Outer	*f*	8–07	5.25	43	2	12	1
Outer	*g*	8–07	1.26	7	3	94	3
Outer	*h*	8–12	1.54	3	0	0	1
Outer	*i*	8–12	4.66	7	23	0	0
Outer	*j*	8–23	9.57	34	30	12	32
Total			25.17	131	59	139	38

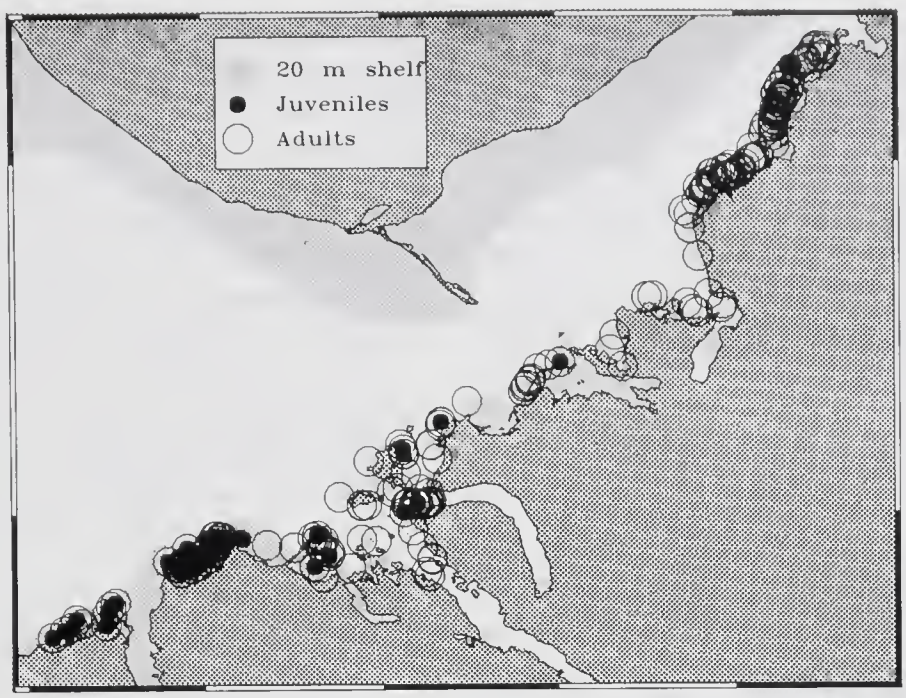

FIG. 2. Distribution of adult (after-hatch-year) and juvenile Marbled Murrelets on surveys conducted in Kachemak Bay, Alaska, on 7–24 August 1996.

fledging period in nearby Prince William Sound, Alaska (Kuletz and Kendall 1998). Pigeon Guillemot fledging dates were similar and were verified from local colony studies (Piatt et al. 1997).

Because we wanted to describe the general distribution of murrelets and our survey routes varied, we pooled all bird counts for a single tally. For both Marbled Murrelets and Pigeon Guillemots we determined the ratio at sea of juveniles to adults and subadults (after-hatching-year birds; AHY). We also calculated an index of juveniles/pair based on counts of juveniles and half the number of adults counted on the same surveys. Piatt and coworkers (1997) obtained detailed observations of Pigeon Guillemots on 60 nests in 9 colonies distributed along the south shore of Kachemak Bay from Glacier Spit to Seldovia Bay.

RESULTS

Fifty-nine of 61 juvenile Marbled Murrelets were found in outer Kachemak Bay and two were found in the inner bay (Table 1). Most of the juveniles in the outer bay were concentrated 0.5–1.0 km offshore, near the mouth of Seldovia Bay (Fig. 2). This area has an extensive kelp bed (*Nereocystis* sp.) and covers an underwater shelf less than 20 m deep. Adult Marbled Murrelets (n = 317; 5 in basic plumage) were distributed throughout Kachemak Bay, with highest densities in the inner bay between Glacier Spit and the bay head (Fig. 2). We found Pigeon Guillemots, both adults (n = 249) and juveniles (n = 62), distributed throughout Kachemak Bay (Table 1).

Juveniles represented 16.1% of all Marbled Murrelets and 24.8% of all Pigeon Guillemots counted. If all of the AHY Marbled Murrelets were breeding, our counts suggest a maximum reproductive success of 0.32 chicks/pair. A more conservative estimate is that only 70% of AHY birds were breeding (Piatt and Ford 1993), and therefore maximum productivity is calculated as 0.46 chicks/pair. For Pigeon Guillemots, the maximum productivity would be 0.50 chicks/pair if all AHY birds were breeding, and 0.71 chick/pair if only 70% were breeding adults.

DISCUSSION

Juvenile Marbled Murrelets in Kachemak Bay showed a clear preference for the kelp beds approximately 4 km on either side of the mouth of Seldovia Bay. This distribution contrasts sharply with the distribution of adult murrelets found throughout the bay. Adult murrelets forage on Pacific sand lance (*Ammodytes hexapterus*) in the inner bay (J. Piatt, unpubl. data), suggesting that the distribution of forage fish was not limiting the distribution of juvenile murrelets.

Why were juvenile murrelets concentrated along the shore in outer Kachemak Bay and in extensive, dense beds of *Nereocystis* kelp? Although exposed relative to the inner bay, the orientation of the shoreline in this area

provided protection from prevailing southwesterly winds. The southwest portion of Kachemak Bay receives upwelled waters from the Alaska Coastal Current entering Cook Inlet from the southeast, and gyres in the outer bay retain nutrients and promote high local productivity (Trasky et al. 1977). The presence of *Nereocystis,* which attach to rocky substrate and grow in water 20–40 m deep where fast currents or upwelling occurs, is often associated with productive waters (Lalli and Parsons 1993). Thus, shallow water, semi-protected seas, the presence of kelp, and locally productive waters appear to combine here to create a favorable nursery area for newly-fledged murrelets. In addition, the kelp made it difficult to see the juveniles, and so may provide protection from avian predators such as gulls and Bald Eagles (*Haliaeetus leucocephalus*), which are common in this area. Large *Nereocystis* kelp beds are not common elsewhere in Kachemak Bay so this feature may be the primary defining characteristic of the nursery.

Juvenile murrelets may use the inner bay temporarily after fledging, and if fledging peaked early in August 1996, it is possible that we missed seeing them before they emigrated to the outer bay. It is also possible that juveniles were absent from the inner bay because few murrelets may breed there now as the result of extensive damage to mature forests from spruce beetle (*Dendroctonus rufipennis*). However, the middle portion of the bay (China Poot to Kasitsna Bay) still has largely intact forests, and while the inner bay is clearly an important foraging area for adults, most juveniles were found in the outer bay. The use of kelp beds in the outer bay by juvenile murrelets appears to be a recurring event; we have observed juvenile murrelets in this area in previous years. Surveys of the entire bay throughout the fledging period would be necessary to determine whether, and if so when, juveniles from throughout the bay move to the kelp beds.

Estimates of Pigeon Guillemot productivity obtained from juvenile surveys at sea compared well to the productivity of guillemots measured from colony-based reproductive studies. Pigeon Guillemots at nine Kachemak Bay colonies in 1996 produced 0.56 chicks/pair, which falls within the range we estimated from counts at sea. The estimate of production we obtained for Marbled Murrelets also approximates that found for Marbled Murrelets throughout their range (0.28 chicks/pair), based on 32 nests followed to completion (Nelson and Hamer 1995). It is noteworthy that our estimate of murrelet production in Kachemak Bay is much higher than those calculated from surveys at sea in areas south of Alaska (e.g., 0.001–0.11 chicks/pair), even after adjustments (0.01–0.17 chicks/pair) for the timing of surveys (Beissinger 1995). This is undoubtedly because we located the nursery area near Seldovia Bay, which accounted for 53 of 61 juveniles we observed on surveys.

While the possibility of juvenile murrelet nurseries has been suggested in some areas (Sealy 1975, Strachan et al. 1995), they have never been documented, and murrelet distribution may not always be as patchy as it appears to be in Kachemak Bay. In southeast Alaska, VanVliet (pers. comm.) observed juvenile murrelets clustered near or in kelp beds in late August in discrete areas of Port Althorp, whereas adults were distributed from Inian Pass to Icy Strait. In Prince William Sound, Alaska, however, juvenile murrelets were evenly dispersed in nearshore waters (relative to local murrelet abundance), with the exception of highly exposed shoreline where they were absent (Kuletz et al. 1997). The areas surveyed in Prince William Sound did not have large kelp beds and were characterized by convoluted, rocky shorelines with numerous protected bays and coves. In addition, the juveniles in Prince William Sound may not travel far in the first two weeks after fledging (Kuletz and Marks 1997; Kuletz, unpubl. data).

These results confirm that surveys at sea provide a reasonable index of productivity for nearshore seabirds such as Pigeon Guillemots and Marbled Murrelets. However, it is important to determine the post-fledging movements of adults and juveniles for any given area of study because adult:juvenile ratios are sensitive to late summer movements of adults and subadults (Kuletz and Kendall 1998). Although our temporal data were limited in this study, we did not find obvious declines in adult numbers in August, such as occurs in Prince William Sound. If juvenile murrelet nurseries can be located, it would facilitate the

use of juvenile densities to measure productivity and thus avoid problems associated with using adult:juvenile ratios (Kuletz and Kendall 1998). If adults remain in an area during the main fledging period where murrelet nurseries exist, surveys at sea may provide a valid measure of absolute productivity, and not just an index of production (e.g., Beissinger 1995).

ACKNOWLEDGMENTS

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"Snorkeling" by the Chicks of the Wattled Jacana

Carlos Bosque[1,3] and Emilio A. Herrera[2]

ABSTRACT.—The chicks of the Wattled Jacana (*Jacana jacana*) exhibited an unusual predator escape behavior in the floodplains of Venezuela. When approached by a human, chicks dove and remained completely immobile while entirely submerged with just the beak protruding vertically above the water line. Since breathing should continue while hiding, we reasoned that it would be advantageous for the bird to have the nostrils placed in a forward position along the bill to facilitate breathing while submerged. To examine this expectation we compared the relative position of the nostrils of the Wattled Jacana with those of species belonging to phylogenetically related Scolopacidae. In accordance with expectations, Wattled Jacanas have nostrils that are placed significantly more forward along the bill than all species of Scolopacidae measured. Nostril placement in species belonging to other phylogenetically related families, Thinocoridae, Pedionomidae, and Rostratulide is also basal as in Scolopacidae. Forward placement of nostrils seems to be a derived character in jacanas. The "snorkeling" behavior of Wattled Jacana chicks is a behaviorally elaborate predator escape mechanism, seemingly accompanied by anatomical adaptations. *Received 16 June 1998, accepted 15 Dec. 1998.*

Predation is often the major mortality factor of young birds and is therefore an important selective force shaping the behavior of young birds and their parents (Rickleffs 1969, Martin 1992). Capabilities of precocial chicks to escape predation or defend themselves from predators are limited. Their chances of predation are largely dependent on actions taken by their parents. When predators approach their chicks, adults frequently perform "distraction displays" that often divert the attention of the predator away from their offspring (Skutch 1976). Safety of precocial chicks also depends upon their small size, concealing coloration and immobility (Skutch 1976). In this note we describe an unusual predator escape behavior exhibited by Wattled Jacana (*Jacana jacana*) chicks and extend information on the hiding behavior of jacana chicks.

The Wattled Jacana inhabits freshwater wetlands with floating and emergent vegetation throughout its range from northern South America and Panama to central Argentina (del Hoyo et al. 1996). Like several other jacanas, Wattled Jacanas show sex-role reversal and a polyandrous mating system (Osborne 1982). Although few details have been reported on Wattled Jacanas (see Osborne and Bourne 1977, Osborne 1982), it is generally assumed to have similar behavioral traits to the Northern Jacana (*J. spinosa*; del Hoyo et al. 1996). Chicks are highly precocious, leaving the nest soon after hatching, but are tended by the male parent. Parental care includes brooding, attending and defending, but not feeding the chicks (Jenni and Collier 1972, Stephens 1984a, Betts and Jenni 1991). Females aid males in defending offspring from potential predators or conspecifics (Jenni and Collier 1972, Stephens 1984a). Heavy predation pressure on eggs and chicks appears to be important in both Wattled and Northern jacanas (Jenni 1974; Osborne and Bourne 1977; Stephens 1984a, b).

Our observations were made on a savanna flooded approximately 40 cm deep, covered with floating and emergent vegetation (*Eichornia* sp., *Hymenachne amplexicaulis*) at Hato El Frio, a cattle ranch and biological reserve in the southern Llanos (floodplains) of Venezuela (7° 46′ N, 68° 57′ W). As E.H. approached a pair of jacana adults with three chicks, one of the adults, presumably the male, performed a typical "broken wing" display, jumping and apparently attempting unsuccessfully to fly. As the observer continued to approach, the parents flew away. When we looked among the vegetation for the chicks they were nowhere to be seen. While searching, we found that what seemed to be an odd looking slender yellowish flower was in fact

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the bill of one of the young jacanas. The chick remained completely immobile while entirely submerged with just the beak protruding vertically above the water. By bringing a hand from below we were able to pick up the bird, which made no attempt to escape nor showed any defense behavior. The chick was in the downy stage.

This hiding behavior should reduce the chances of detection by predators or aggressive conspecifics. For it to be effective, the chick should remain motionless underwater for an unpredictable length of time. In order to continue breathing while submerged it would be advantageous to have the nostrils placed toward the tip of the bill.

To examine this prediction, we compared the relative position of the nostrils of the Wattled Jacana with those of phylogenetically related species. Of the four other families in the same parvorder (Sibley and Monroe 1990) only Scolopacidae occur in Venezuela and specimens were available in bird collections. We selected at random 6 of the 12 genera of Scolopacidae that occur in the country (Meyer de Schauensee and Phelps 1978) and one species from each of these, except for speciose genus *Calidris* from which we chose two species. In 10 individuals of each species we measured the length of the exposed culmen (EC) and the distance between the posterior margin of the right nostril and the tip of the bill (NT). Specimens, selected at random, were measured at the Phelps Ornithological Museum in Caracas with calipers to 0.1 mm. For jacanas we measured separately adults, juveniles, and the one downy chick in the collection. The exposed culmen was measured from the base of the frontal shield where it rises more abruptly. From those measurements we calculated an index (I) to describe the relative position of the nostrils along the bill:

$$I = (EC - NT)/EC$$

The value of this index should be zero in those species in which the nostrils are placed at the base of the bill and closer to one the nearer the nostrils are to the bill tip. Statistical analyses were done with SYSTAT 7.0 for Windows (Wilkinson 1997).

Mean relative position of the nostrils differed between species (Fig. 1; Single Factor ANOVA on the arcsine-transformed data: $P < 0.001$, $F = 143.632$, df = 7); the single jacana chick and juveniles were not included in this comparison. A Tukey HSD *a posteriori* test revealed a number of significant differences between species ($P < 0.05$; Fig. 1). Wattled Jacana nostrils are placed significantly more forward along the bill than all species of Scolopacidae measured (Fig. 1). Nostrils were also placed forward on juveniles and one newly hatched downy chick.

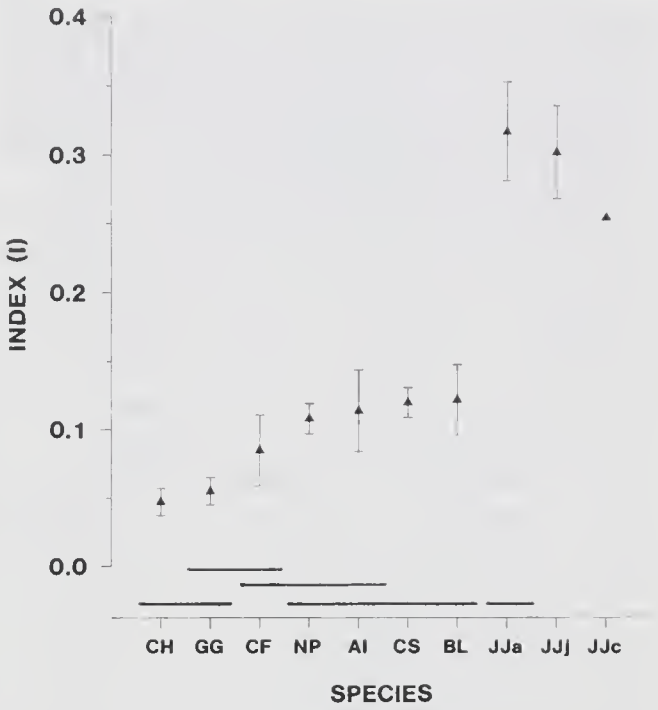

FIG. 1. A comparison of the relative position of the nostrils along the bill between *Jacana jacana* and several species of Scolopacidae. Mean Index values (± SD), see text for definition of the Index. Species are: CH = *Calidris himantopns*, GG = *Gallinago gallinago*, CF = *Calidris fuscicollis*, NP = *Nmenins phaeopus*, AI = *Arenaria interpres*, CS = *Catoptrophorus semipalmatus*, BL = *Bartramia longicanda*, JJa = *Jacana jacana* (adults), JJj = *J. jacana* (juveniles), JJc = *J. jacana* chick. $n = 10$ in all cases, except for the single *J. jacana* chick. Horizontal lines above species labels indicate similarity between the index mean of those species (from Tukey HSD test). *Jacana jacana* juveniles and the chick were not included in the test.

Nostril placement in species belonging to families phylogenetically related to the Jacanidae, but not available to us, can be seen in photographs in del Hoyo and coworkers (1996). Both species of Rostratulidae (belonging in the same superfamily with Jacanidae) have nostrils placed basally (del Hoyo et al. 1996:293–299). In the Plains-wanderer (*Pedionomus torquatus*, Pedionomidae), the posterior end of its longish narina is clearly set

back (del Hoyo et al. 1996:535–536). The cornaceous flaps covering the nostrils of the Thinocopridae (*Thinocorus* spp., *Attagis gayi*) appear to be placed at the base of the bill also (del Hoyo et al. 1996:539–543).

It appears that basal placement of the nostrils is ancestral in the group and that forward displacement in jacanas is a derived character. We cannot assert that breathing while submerged was an important selective force in the forward displacement of jacana nostrils, but their current position should facilitate it.

Young of jacanas are known to avoid predators or aggressive conspecifics by taking to water and snorkeling behavior is shared with other species. The chicks of the Northern Jacana, which is considered to form a superspecies with the Wattled Jacana (del Hoyo et al. 1996), have been reported to swim (Gilliard 1967), to hide in the water (Stephens 1984a), and to submerge with only their bills and the tops of their heads showing above the surface (Miller 1931). The hiding behavior of young Pheasent-tailed Jacanas (*Hydrophasianus chirurgus*) from India and Asia seems similar; chicks "may freeze while hiding under a leaf or even while completely submerged except for the bill" (Johnsgard 1981:40). The chicks, and sometimes even the adults, of the Lesser Jacana (*Microparra capensis*) of Africa are also known to submerge with only their bills out of the water (Maclean 1972). Since snorkeling seems to be accompanied by anatomical adaptations, it is likely that those species have forward displaced nostrils also. In fact, this seems to be the case in the Northern (del Hoyo et al. 1996:277) and Pheasent-tailed Jacana (drawing in del Hoyo et al. 1996:288). For the Lesser Jacana it is difficult to judge from available pictures. Other species of jacana for which we do not have information on snorkeling behavior also have nostrils placed in forward position along the bill, most notably the African Jacana (*Actophilornis africanus*; del Hoyo et al. 1996:281). A broader survey would be necessary to establish if snorkeling and forward placement of the nostrils is shared by all species of the family.

In similar aquatic habitats in the central Llanos of Venezuela, the young of at least three other species swim or dive, although adults do not: the altricial nestlings of Hoatzins (*Opisthocomus hoazin*; Strahl 1987) and Greater Anis (*Crotophaga major*; Lau et al., in press) jump from their nest and swim or dive in the water below; the precocial chicks of Purple Gallinules (*Porphirula martinica*) dive when threatened (Zaida Tárano, pers. comm.). Interestingly, the latter and congeneric *P. flavirostris* have nostrils displaced forward along the bill (pers. obs.).

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Rapid Long-distance Colonization of Lake Gatun, Panama, by Snail Kites

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ABSTRACT.—The distribution of the Snail Kite (*Rostrhamus sociabilis*) is closely tied to that of apple snails (*Pomacea* spp.), its nearly exclusive food. Before the early 1990s, the species occurred in Panama primarily as a vagrant. Apple snails were introdueed to Lake Gatun in central Panama in the late 1980s, and by 1994 Snail Kites had colonized the lake from population sourees at least 350 km away and initiated breeding. Since 1994 the population has increased rapidly and the species can now be found throughout the lake. *Received 7 Oct. 1998, accepted 6 Jan. 1999.*

The Snail Kite (*Rostrhamus sociabilis*) is a highly specialized raptor that ranges from southern Florida and Mexico, through Central America, to Bolivia, northern Argentina and Uruguay (Beissinger 1988). Its distribution is closely tied to that of apple snails (*Pomacea* spp.), which form its diet almost exclusively (Beissinger 1988). The kite uses its exceptionally thin upper mandible to extract snails from their shells (Snyder and Snyder 1969). Other species of snails, turtles, crabs and other items are taken on occasion (Beissinger 1990a, Snyder and Kale 1983, Sykes and Kale 1974). The species is nomadic, moving in response to changes in the availability of its favored prey because of fluctuating water levels (Sykes 1979, 1983; Beissinger and Takekawa 1983, Takekawa and Beissinger 1989).

Snail Kites are rare in southern Central America, and there have been only seven previous reports from Panama (Ridgely and Gwynne 1989). The sole Panama specimen, an immature female, was collected near the Colombian border at Permé, near Puerto Obaldía, San Blas Province, in 1929 (Wetmore 1965). There were four reports of single birds, all either females or immatures, at marshes near Panama City, in 1971, 1973, 1977, and 1979. There were two reports from Chiriquí province in western Panama; an adult male and a female or immature near Gualaca in 1965, and several pairs and a nest in a marsh near Remedios in 1973, the latter being the only previous report of breeding activity in Panama (Ridgely and Gwynne 1989). The closest significant populations of Snail Kites to Panama are in western Colombia, on the west side of the Gulf of Urabá (Hilty and Brown 1986), about 350 km from the Panama Canal area, and the Tempisque Basin in northern Costa Rica (Stiles and Skutch 1989), approximately 650 km away.

STUDY AREA

Lake Gatun (420 km^2) is an artificial lake ereated by the damming of the Chagres River to form the ecntral part of the Panama Canal in 1914. The lake level is controlled by the Panama Canal Commission, and may vary sevcral meters between wet and dry seasons as water is relcased when ships pass through the locks. The Canal area experiences a strong four-month long dry season from mid-December to mid-April.

The introduced aquatie plant *Hydrilla verticillata* is a major problem in the lake. It apparently first became established in the late 1920s or early 1930s, and had

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become a significant problem by the 1960s (Maturell and Salazar 1994). Rooting in shallow water, it now occurs in huge beds in many parts of the lake.

The apple snail *Pomacea lattrei* was introduced to Panama from Guatemala in the early 1980s by Panama's National Directorate of Aquaculture. Snails were established at a research station at Divisa, Herrera Province, approximately 130 km west of Lake Gatun, for use in rural aquaculture programs. Between 1986 and 1988, the owner of a sportfishing business in the town of La Arenosa on the southwestern arm of Lake Gatun obtained 15 snails from the Divisa station and introduced them to a small artificial pond next to Lake Gatun. After they had reproduced, she distributed some to neighbors and introduced others into the lake. A few months later it was noticed that the snails were feeding on and reducing the abundant *Hydrilla* around the community's public dock and in surrounding areas. Residents of other lakeside communities began deliberately introducing snails to their areas in an effort to control *Hydrilla* (Maturell and Salazar 1994), a major impediment to small boat travel. The snails are also used for food by some local people.

Surveys by the Panama Canal Commission found that the snails were distributed throughout the southeastern arm of the lake by 1991, were in the northwestern part by 1992, and had reached the town of Gamboa at the east end of the lake by 1993. In some areas *Hydrilla* cover was reduced by as much as 94% in three years. Deliberate introduction by humans evidently allowed the snail to disperse quickly around the lake. The snails also spread by floating in currents and by egg masses fixed to floating vegetation, logs, and boats (Maturell and Salazar 1994).

A native species of apple snail, *Pomacea cumingi*, occurs in the Canal area. It is a bottom-dwelling species that typically occurs in low densities. It mostly inhabits small streams, but is sometimes found in larger rivers. The combination of habitat, bottom dwelling habit, and low density evidently makes this species unsuitable as prey for Snail Kites (F. G. Thompson, pers. comm.).

RESULTS

M. Santamaría (pers. comm.), a game warden at the Barro Colorado Nature Monument, a reserve managed by the Smithsonian Tropical Research Institute, first observed unusual hawklike birds eating snails in Gigante Bay, south of Barro Colorado Island, in May or June 1994. On 3 February 1995 Santamaría and I visited an area where he had recently seen birds building nests in Guindilla Cove, a narrow inlet about 1500 m long on the south shore of Gigante Bay. We saw at least 14 Snail Kites in the cove at that time, including at least two adult males in black plumage. The remaining birds were in brown plumage. Immatures and adult females have brown plumage and cannot reliably be distinguished in the field (S. Beissinger, pers. comm.).

At four locations we observed nests consisting of loose platforms of twigs at various stages of construction. One small vine-covered tree standing in water (Site 1) had seven nests while the other sites had one nest each. No eggs or chicks were evident at that time, although we could not see the contents of high nests. Santamaría recently had seen birds bringing twigs to add to the nests.

The area was visited again on 20 May 1994 by D. and L. Engleman. They did not see any active nests at Site 1, but at least 17 kites were soaring or perched in the area. They observed five nests at another site (Site 2) about 300 m north of Site 1. These were located on a small island composed of *Annona glabra* shrubs overgrown with vines. Three nests were complete, one with two eggs and another with at least one egg and perhaps more. A third nest appeared to have eggs but they could not be counted. The remaining two nests were under construction and were visited by birds in brown plumage carrying twigs. At least 20 kites were present at this site, yielding a total of at least 37 in the cove (D. and L. Engleman, pers. comm.).

I visited Guindilla Cove again on 15 July 1994. At that time seven nests were present at Site 2. Two nests had three well-feathered nestlings, while two more fledglings were perched together on a branch near a third nest. Three other birds which took flight from the island had very short tails and appeared to have recently fledged. On 27 August 1994 two nests at Site 1 each had a single large downy young. No active nests were present at Site 2, but I saw two birds that apparently had recently fledged. On 14 October no activity was seen at Site 1, but three apparently recently fledged birds were present at Site 2. On this date I also surveyed several other areas in Gigante Bay that I had not previously investigated. One nest with two small nestlings was found near an island at the mouth of Guindilla Cove, and a second nest with two fledglings on the verge of flying was found on a large *Annona glabra* island about 3 km west of Guindilla. Approximately 15 adults and three apparently recently fledged young were also seen at this site.

DISCUSSION

Apple snails probably reached the area of Gigante Bay in 1991 (Maturell and Salazar 1994). I am certain no kites were present in the area before 1992, because I made three surveys of the shoreline of parts of the bay by canoe in 1991 and 1992, and surveyed Guindilla Cove itself on 23 August 1992. Guindilla Cove probably was colonized by kites in either 1993 or 1994.

In 1995, in the central part of the lake near the Panama Canal channel, Snail Kites were restricted to Gigante Bay, based on information from Smithsonian game wardens and researchers who worked on the lake. Kites were rarely if ever seen at the Smithsonian research station on the north side of Barro Colorado Island 4 km away.

Since 1995, kites have been seen more often in other parts of Lake Gatun and the Canal area in general, ranging from the northern end of the lake near the Gatun Locks to Miraflores Locks near the Pacific entrance to the Panama Canal. Although no comprehensive surveys of kite distribution and numbers have been made, Snail Kites appear to have spread throughout the lake and occur wherever suitable habitat is present.

In 1995 nest construction evidently began in January, during the early dry season. A few small nestlings were still present in mid-October, during the late rainy season. These latter birds would probably have fledged in November, so that in 1995 the breeding season was at least 10 months long. In Florida, the main nesting season is January–August, peaking in February–June, although in years of high water breeding may begin in December and extend to September (Beissinger 1986, 1988; Snyder et al. 1989). Nesting seasonality is poorly known elsewhere in the tropics, but may be tied to the rainy season. Nesting takes place during the wettest period in Surinam, Argentina and Venezuela (Beissinger 1988).

At Gigante, clutch or brood size ranged from one to three. In Florida, clutch size presently ranges from one to three with the latter much more frequent. However, clutch size appears to have declined historically in Florida, with four-egg clutches previously having been common (Beissinger 1986). The decline may be attributable to habitat deterioration. Although there are few data, clutch size elsewhere in the kite's range seems typically to be two to three, although four-egg clutches often occur in Argentina (Beissinger 1990b) and clutch size may range up to six (Beissinger 1988). Despite a presumably superabundant food supply at Gigante in 1995, there was no evidence that kites increased their clutch size in response.

The Snail Kite colony in Guindilla cove increased from no birds in 1992 to at least 37 in 1995, an extraordinarily high rate of increase if only a single founding pair had been involved. Because Kites are highly sociable, initial colonization could have been by a small flock of birds rather than a single pair. It is possible that Guindilla Cove was not the initial site of colonization of Lake Gatun. Snails were present in the southwestern arm of the lake by the late 1980s. Kites could have colonized that area first, and then spread to Guindilla. The southwestern arm of the lake is large and remote from population centers, so a colony there could easily have gone undetected.

Nevertheless, Snail Kite populations increase rapidly under favorable conditions (Snyder et al. 1989, Beissinger 1995), such as the essentially unlimited food supply Lake Gatun would have offered the first colonists. The age at first reproduction in Snail Kites is very low, with some females nesting at 10 months. In favorable years in Florida, the breeding season may last up to 10 months, and some kites may re-nest and raise second broods (Beissinger 1986, Snyder et al. 1989). Parents of either sex may desert a nest leaving the other member of the pair to continue to raise the young alone (Beissinger and Snyder 1987). The remaining parent almost always is able to rear the young to independence by itself, while the deserting parent has the opportunity to re-nest with another partner.

The rapid colonization by Snail Kites of Lake Gatun and subsequent population expansion provides an interesting example of the dispersal capabilities of this highly opportunistic species. The most likely source of colonizing birds would have been the Colombian population, approximately 350 km from Lake Gatun. This population is much closer than the one in Costa Rica, and there are several large areas of freshwater habitat, including

Lake Bayano and several large rivers, in the intervening area. Dispersers discovered the newly suitable habitat of Lake Gatun within only a few years after the introduction of their preferred food, and rapidly spread throughout the available area.

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The "Significant Others" of American Kestrels: Cohabitation with Arthropods

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ABSTRACT.—We examined the arthropod fauna that coexists in nest boxes with American Kestrel chicks (*Falco sparverius*) in northwestern New Jersey. Of the seven arthropod species present, five were scavenging beetles, including carrion beetles (*Silpha inaequalis*), hister beetles (*Atholus americanus* and *Phelister subrotundus*), dermestid beetles (*Dermestes caninus*), and skin beetles (*Trox foveicollis*), which apparently were attracted to prey remains that accumulated in the nest boxes. Arthropod density and species richness were significantly greater for nest boxes in which kestrels bred than for unoccupied nest boxes. *Received 30 June 1998, accepted 16 Nov. 1998.*

Studies of the association between American Kestrels (*Falco sparverius*) and arthropods have focused primarily on (1) the occurrence of these invertebrates in kestrel diets and the predatory behavior kestrels direct toward them and (2) parasitic arthropods reported to infest kestrels (for reviews see Sherrod 1978 and Smallwood and Bird in press, respectively). However, arthropods interact with kestrels in another functional role, that of symbiotic scavengers. Kestrels are a cavity nesting species; typical brood size is four or five, and the nestling period lasts about 30 days (Johnsgard 1990). During this time prey remains, regurgitated pellets, and other organic material accumulates in the nest cavity (Balgooyen 1976; Smallwood, pers. obs.). Balgooyen (1976) observed dermestid beetles (*Dermestes* spp.) in each of approximately 40 kestrel nests in northern California and commented on their role in nest sanitation. The objectives of the present study were to examine the arthropod community that coexists with kestrels breeding in nest boxes in New Jersey and to compare them to the invertebrate fauna in nest boxes not occupied by kestrels.

STUDY AREA AND METHODS

The study area was located in rural northwestern New Jersey, bordered to the north and west by the Kittatinny Ridge and Delaware River, and to the east and south by residential and commercial development. This area is characterized by mixed agriculture, including corn, hay, and cattle production, and forestland in the ridge and valley physiographic region (Sauer et al. 1997). Sixty wooden nest boxes (internal dimensions: 20 × 23 cm floor, ca 34 cm in height) were erected in open habitats in Sussex County (centered approximately 41° 11′ N, 74° 38′ W) between 1 April 1995 and 25 April 1997, and 69 nest boxes in Warren County (approximately 40° 47′ N, 75° 04′ W) between 5 August 1995 and 26 March 1997. Because kestrels do not bring any nesting material into the nest cavity (Bird and Palmer 1988), we covered the floor of each nest box with approximately 6 cm of wood shavings to provide a cushion and insulation for the eggs.

Each nest box was monitored at 4-week intervals from 23 March through 13 July 1997 to determine occupancy status; a nest box was considered occupied by breeding kestrels if at least one egg was observed. Kestrels require 7–9 days to produce and 28–30 days to incubate a clutch (Bird and Palmer 1988); thus, all kestrel nesting attempts were discovered during the laying or incubation stage. Nest boxes in which kestrels bred (herein "kestrel nest boxes") were visited 3–7 times throughout the nesting attempt. During the final visit chicks were banded and the bedding (including cohabiting arthropods, prey remains, pellets, and any other material) was collected and replaced with fresh wood shavings. Final visits occurred between 21 June and 1 August 1997 when nestlings were 16–23 days old (75% were 20–22 days old).

In addition to kestrels, other vertebrates that bred in the nest boxes included five avian species (Great Crested Flycatcher, *Myiarchus crinitus*; Tree Swallow, *Tachycineta bicolor*; Eastern Bluebird, *Sialia sialis*; European Starling, *Sturnus vulgaris*; and House Sparrow, *Paser domesticus*) and four species of mammals (eastern gray squirrel, *Sciurus carolinensis*; red squirrel, *Tamiasciurus hudsonicus*; southern flying squirrel, *Glaucomys volans*; and white-footed mouse, *Peromyscus leucopus*). Only four nest boxes remained unoccupied by any vertebrate species, including kestrels, during the breeding season (herein "unoccupied nest

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TABLE 1. Taxonomy and abundance of arthropods co-inhabiting nest boxes with American Kestrel broods in northwestern New Jersey.

Taxonomy	Nest boxes occupied (%)	Individuals per occupied[a] nest box		
		Mean	SD	Range
Arachnida				
Araneida				
Aglenidae				
Tegenaria derhamii, funnel spider	6.3	1.0	0.0	1–1
Insecta				
Coleoptera				
Silphidae				
Silpha inaequalis, carrion beetle	68.8	41.0	30.8	3–114
Histeridae				
Atholus americanus, hister beetle	31.3	4.8	3.4	2–9
Phelister subrotundus, hister beetle	37.5	8.8	11.1	1–24
Dermestidae				
Dermestes caninus, dermestid beetle	12.5	5.0	5.7	1–9
Trogidae				
Trox foveicollis, skin beetle	6.3	3.0	0.0	3–3
Hymenoptera				
Formicidae				
Camponotus pennsylvanicus, black carpenter ant	6.3	1.0	0.0	1–1

[a] Nest boxes in which a particular arthropod species was present.

boxes"). The bedding was collected from unoccupied nest boxes on 11 and 13 July 1997.

All bedding samples were stored at −22° C in airtight plastic bags to preserve any arthropod specimens present. We subsequently extracted all arthropods visible at 1.75× magnification, preserved them in 70% ethanol, and identified them with information from Comstock and Gertsch (1948), Emerton and Frost (1961), Borrer and White (1970), Headstrom (1977), Kaston (1978), Milne and Milne (1980), and Arnett (1985).

Data on arthropod density and richness were tested for normality. Because significant deviations were detected, we used nonparametric statistical treatments exclusively, including the Wilcoxon rank sum test, Spearman's correlation coefficient, and Fisher's exact test (Snedacor and Cochran 1980). Analyses were performed using SAS 6.12 on a Sun Solaris 2.6 platform.

RESULTS

A total of 567 individual arthropods were extracted from the bedding collected from 16 kestrel (Table 1) and four unoccupied nest boxes. Arthropod density ranged from 0 (for two kestrel and two unoccupied nest boxes) to 115 individuals in one kestrel nest box. Mean arthropod density for kestrel nest boxes (35.3 ± 31.0 SD) was significantly greater than that for unoccupied nest boxes (0.50 ± 0.58 SD; two-tailed Wilcoxon rank sums test: $Z = 2.421$, $P = 0.016$). Maximum arthropod density in unoccupied nest boxes was 1: a crab spider (Thomsidae, *Xysticus triguttus*) in one nest box and a European earwig (Forficulidae, *Forficula auricularia*) in one other.

Species richness per nest box ranged from 0–3 and mean richness for kestrel nest boxes (1.69 ± 0.87 SD) was significantly greater than that for unoccupied nest boxes (0.50 ± 0.58 SD; two-tailed Wilcoxon rank sum test: $Z = 2.258$, $P = 0.024$). No significant correlation was detected between arthropod species richness and kestrel brood size ($r_S = 0.17$, $P > 0.05$, $n = 16$), or between kestrel brood size and arthropod density ($r_S = -0.14$, $P > 0.05$, $n = 16$).

DISCUSSION

Of the seven arthropod species observed in kestrel nest boxes in New Jersey, five (all the beetles) are considered scavengers (Headstrom 1977), and the carpenter ant is known to forage primarily on insects (Palmer 1975). The dermestid beetle (*D. caninus*), found in two of the nest boxes, was the same species commonly used in museums for cleaning flesh from skeletal specimens (Headstrom 1977).

The mean and maximum densities of arthropods in the kestrel nest boxes in New Jersey were considerably less than those observed in northcentral Florida (Smallwood,

pers. obs.). In Florida, dermestid beetles and other species typically occurred in large numbers, such that by the end of the nestling period the substrate upon which the chicks stood visibly pulsated as the result of the motion of these arthropods. In an experiment to determine if high arthropod densities in nest cavities discourages second clutches, Smallwood (unpubl. data) replaced the bedding for a randomly selected group of nest boxes after kestrel chicks had fledged. Kestrels renested in 11.1% of the cleaned nest boxes (n = 27) and 14.0% of the control nest boxes (n = 50); these percentages were not significantly different (one-tailed Fisher's exact test, P = 0.76).

We saw no evidence of kestrel chicks bitten or otherwise harmed by the arthropods living in the New Jersey nest boxes. Rather, the removal of much of the decaying organic material (i.e., uneaten scraps of insects, small birds, and rodents) may benefit kestrels by reducing the risk of disease or infestation with parasites. The significant difference in the number and species of arthropods present between kestrel and unoccupied nest boxes, and the fact that nearly all the arthropods were scavengers, suggest that breeding kestrels are producing the conditions that attract these invertebrates.

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Barred Owl Nest in Attic of Shed

C. Stuart Houston[1]

ABSTRACT.—Barred Owls (*Strix varia*) nested in the attic of a shed during 12 out of 13 years at Flotten Lake, Saskatchewan. Twelve nestlings were banded in five seasons. Although two species of *Strix* are known to nest in buildings in Europe, this appears to be the first such instance in North America. *Received 7 Oct. 1998, accepted 7 Jan. 1999.*

For twelve out of thirteen years (1980–1992), Barred Owls (*Strix varia*) nested in the same attic of a shed along Flotten Lake, Saskatchewan. Prior to this, Barred Owls had never been reported to use a building for nesting purposes. Furthermore, this example represents the longest continuous use of one nest site by this species, reported to date in Saskatchewan.

Barred Owls apparently moved into central Saskatchewan from adjacent Manitoba in the 1950s. They occupied a relatively narrow band of mixed forest, most often near lakes and rivers. The first Saskatchewan nest was located in 1961 (Houston 1959, 1961). In the only Barred Owl nesting study conducted in Saskatchewan, Mazur and coworkers (1997) found nests only in mature forest: 6 in broken tree snags, 4 in broken limbs, 2 on squirrel platforms, 2 on stick nests, and 1 on a witch's broom platform. Of these nests, 10 were in deciduous trees and 5 were in conifers.

On 15 May 1988, I first visited an abandoned shed (Fig. 1), built in 1946 in a 1.6-ha man-made clearing located in mixed old-growth forest near the shores of Flotten Lake, Saskatchewan (54° 30′ N, 108° 30′ W). During the visit I banded three half-grown Barred Owl nestlings. The property owners, Mr. and Mrs. D. Mazuren, had observed Barred Owls nesting on the attic floor in this building every year except one since 1980. Consequently, 1988 was the eighth year of use in nine years. During other times of year, the owls were seen in nearby trees but never perched on or in the buildings. On 3 June 1989, we again banded three young and took photographs. On 11 June 1990, we banded the single nestling raised that year; on 28 May 1991, three nestlings; and on 30 May 1992, two nestlings (only 2 eggs had been present on 19 April). The shed attic has not been used since.

The 12 years of use is similar to the 10 consecutive years that Barred Owls used a deep cavity in a dead oak in southeastern Massachusetts (Bent 1938). I have found no other records of Barred Owls using buildings for nest sites, although they use artificial nest boxes in Wisconsin and Minnesota (Johnson and Follen 1984). In Europe, other species of

FIG. 1. Author banding young Barred Owls in the attic of a shed. Photograph by D. G. Miller.

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Strix use buildings, especially barns, as nest sites. The Tawny Owl (*Strix aluco*) uses buildings as nest sites 15% of the time, similarly, the Ural Owl (*Strix uralensis*) nests in buildings 2–4% of the time (Mikkola 1983).

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Double Brooding in the Long-eared Owl

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ABSTRACT.—Owls in the family Strigidae typically raise no more than one brood per year. We documented what apparently is the first unequivocal case of double brooding in Long-eared Owls (*Asio otus*). A banded female raised 12 young in two nesting attempts compared with a mean of 5.3 young for three single-brooded females that nested in the same grove. Two factors may have influenced the occurrence of double brooding: the first nest was initiated unusually early in the year (mid-February) and food availability (in the form of voles) was high. The rare description of double brooding in Long-eared Owls may be due to the difficulty of detecting it. Alternatively, double brooding may be uncommon because it is seldom an economically viable strategy. Factors that would select against double brooding include low probability of recruitment of the first-brood young, and reduced survival and fecundity of the adults. *Received 17 Sept. 1998, accepted 29 Dec. 1998.*

The number of young raised per year is an important component of an individual's lifetime reproductive success. Double brooding, in which a second brood is attempted after a successful first attempt, is a viable strategy if the increase in fitness that results outweighs the cost of any reduction in future survival or fecundity of the adults and their young from the first brood. The occurrence of double brooding may be influenced by factors such as length of the breeding season, food availability, growth rates of the young, and the duration and quality of parental care (e.g., Drent and Daan 1980, Askenmo and Unger 1986, Tinbergen and van Balen 1988).

Double brooding is relatively rare in raptors, presumably because the length of the breeding cycle and extended postfledging care preclude its occurrence (Newton 1979, Morrison 1998). Among nocturnal raptors, double brooding occurs regularly in Barn Owls (*Tyto alba*; Marti 1992, 1997) and occasionally in Florida Burrowing Owls (*Athene cunicularia floridana*; Millsap and Bear 1990) and Boreal Owls (*Aegolius funereus*; Kellomäki et al. 1977, Solheim 1983). During a study of breeding Long-cared Owls (*Asio otus*), we documented a female that raised two broods during the same nesting season. Here, we describe the event and discuss factors that may have influenced its occurrence.

STUDY AREA AND METHODS

The study area is a small grove (ca 2 ha) of quaking aspens (*Populus tremuloides*) and black hawthorns (*Crataegus douglasii*) located about 16 km west of Polson, Lake County, Montana (47° 40′ N, 114° 20′ W). The elevation at the site is 888 m, and the nesting

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grove is surrounded by grasslands and agricultural fields (mostly hay). The 11 Long-eared Owl nests that occurred in the grove in 1997 and 1998 were in old nests of Black-billed Magpies (*Pica pica*) and American Crows (*Corvus brachyrhynchos*).

Adults were captured at night in mist nests placed near the nest or at dusk with the aid of a plastic decoy of a Great Horned Owl (*Bubo virginianus*). Captured adults were classified as after hatching year (AHY) or after second year (ASY) based on the absence or presence of two generations of secondaries, respectively (see Pyle 1997). During the breeding season, the sex of most adults can be determined in the field by differences in plumage coloration and in the hand by presence or absence of an incubation patch (Marks et al. 1994).

RESULTS

On 16 February 1998, we observed a female Long-eared Owl incubating at a nest (PSNII) about 25 m north of a nest that had produced young the previous year. The male was roosting nearby, but we could not determine whether he was banded. Three of the five Long-eared Owl nests that occurred in the grove in 1998 were initiated in February; PSNII appeared to be the earliest of these nests. On 2 April, JSM captured the adult (AHY) female (band no. 951) by hand at PSNII as she was brooding seven young that ranged in age from about 1 to 3 weeks old. Based on the estimated age of the chicks and an incubation period of 28 days (Marks et al. 1994), female 951 would have initiated egg laying on 12 February, and the oldest chick would have hatched on 12 March. Other duties prevented us from catching the mate of female 951 during this nesting attempt.

During a visit to the nesting grove on 25 June, we found a new Long-eared Owl nest at the northern edge of the grove 28 m from nest PSNII. A female was brooding small chicks that appeared to be about 2 weeks old, and a male was flushed from the same roost site typically used by the PSNII male earlier that spring. We returned to the nest on the evening of 30 June and captured the female in a mist net placed directly in front of the nest. She proved to be 951, the same female that had fledged seven chicks earlier in the spring. The next morning we banded her five chicks, which were about 2 to 3 weeks old. Female 951 was very aggressive as we handled her chicks, diving and perching within 1 m of us and enabling us to observe her band and to note her pattern of flight-feather molt that we had confirmed in the hand the previous night (4 primaries and 2 secondaries growing on each wing). Also at this time, we noticed that her mate was banded. After several attempts, we succeeded in capturing the male on the evening of 13 July, at which time the oldest chicks were capable of short flights from tree to tree. The male proved to be no. 914, the same male that had nested at this site in 1997. Female 951 was still present, and both adults presumably were provisioning their fledglings. Interestingly, male 914 had not started flight-feather molt.

Female 951 fledged 12 young (defining "fledging" as capable of sustained flight; Marks 1986) in two nesting attempts compared with a mean of 5.3 young (range 5 to 6) produced by the other three pairs that nested in the grove in 1998. The estimated time between the initiation of 951's two nesting attempts was 90 days (i.e., 12 February and 12 May). At the time 951 initiated her second clutch, the oldest offspring from her first brood would have been about 6 weeks old.

DISCUSSION

Several records of double brooding by Long-eared Owls have been reported in Europe (Reinsch and Warncke 1968, Rinne 1981, Scott 1997), but in each case the evidence was circumstantial. To our knowledge, ours is the first report of double brooding in Long-eared Owls based on a banded individual.

We suspect that weather and food availability played a major role in this case of double brooding. The winter of 1998 was unusually mild in western Montana. The ground at the study area was virtually free of snow from January onward (pers. obs.), and the mean temperature in February was 2.1° C above normal at the Kerr Dam weather station 13 km from the study area (data obtained from the National Climatic Data Center). In addition, voles (*Microtus* spp.) were abundant in winter and spring; we saw many during the day, and other vole-eating raptors [i.e., Northern Harrier (*Circus cyaneus*), Rough-legged Hawk (*Buteo lagopus*), and Short-eared Owl (*Asio flammeus*)] were numerous in the study area. The mild weather and abundant food probably induced Long-eared Owls to nest in February, which is very early for this species (see Marks

et al. 1994). The continued high numbers of voles in summer provided an opportunity for double brooding, at least for one of the three pairs that began nesting in February.

In general, the incidence of second nesting attempts in facultatively double-brooded species is negatively correlated with the laying date of the first clutch (e.g., Smith et al. 1987, Geupel and DeSante 1990, Morrison 1998). Our case agrees with this finding, but it raises the question of why the other two Long-eared Owl pairs that nested early did not raise a second brood. One possibility is that the phenotypic quality of the double-brooded pair was high relative to the other pairs (see Verboven and Verhulst 1996). Although we have no objective measure of phenotypic quality in the Long-eared Owls we studied, we note that the male of the second nesting attempt had bred successfully at the site in the previous year (the other males did not breed there in 1997), and the female that nested twice was in good physical condition and was unusually aggressive. Indeed, during her first attempt she attacked JSM when he entered the nest. Moreover, the ratio of her body mass (g) to wing length (mm) at first capture (1.33) was higher than that of all but one of the other eight females captured late in the brooding-rearing period in 1997 and 1998 ($\bar{x}$ = 1.11 ± 0.13 SD, range 0.98–1.34). The local experience of the male and the physical condition and aggressiveness of the female are consistent with the notion that they were high-quality individuals relative to the other early nesters in the grove.

Double brooding in Long-eared Owls may be more common than previously thought. Alternatively, it may indeed be rare because it is seldom an economically viable strategy. For instance, the fitness gain from double brooding would be marginal if the probability of recruitment of first-brood young is low (i.e., because of reduced care from parents that direct their efforts to a new brood), or if future survival and fecundity of the adults are reduced. Female Long-eared Owls in Idaho deserted their broods when the young were 6.5 to 8 weeks old, and males continued to care for the young until they were 8.5 to 11 weeks old (Ulmschneider 1990). If parental care of this duration is typical in Long-eared Owls, then the first of the two broods would have received a normal amount of parental care (the second clutch was started when the oldest chicks from the first nest were 6 weeks old) only if the female changed mates between nesting attempts (and the male continued to care for the young), or if one or both parents continued to provision the first brood while starting the second (an unlikely occurrence given that the male must provide food to the incubating female). Moreover, the timing of second broods could interfere with the molt schedule of adults. Long-eared Owls generally begin molting in early June soon after breeding (Marks et al. 1994). The male attending the second brood had not started flight-feather molt in mid-July, suggesting that his molt was delayed because of the late breeding effort. Delayed molt potentially could influence survivorship and fecundity (see Pietiäinen et al. 1984, Kjellén 1994).

In conclusion, double brooding appears to be rare in Long-eared Owls, and it probably occurs only when first nests are initiated early and food availability is high. Nothing is known about how double brooding affects recruitment of young from first versus second broods, or whether it affects the survivorship and future fecundity of the parents. Whether double brooding is a viable strategy in Long-eared Owls remains to be determined from additional research.

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Planning to Facilitate Caching: Possible Suet Cutting by a Common Raven

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ABSTRACT.—Many species of birds feed on suet in winter. As far as is known, they all take bite-sized chunks by pecking into this food randomly and/or they tear off protruding pieces. I compared the peck-marks left on suet by Blue Jays (*Cyanocitta cristata*) and American Crows (*Corvus brachyrhynchos*) with those left by Common Ravens (*Corvus corax*). Although most ravens feed like jays and crows, at least one individual made distinct grooves, aligning dozens of consecutive pecks, apparently to cut transportable chunks off large suet blocks. *Received 28 Aug. 1998, accepted 7 Jan. 1999.*

The Common Raven, *Corvus corax*, is a feeding generalist (Bent 1946, Ratcliffe 1997). Ravens feed on carrion (Ewins et al. 1986), fruit, grain, eggs, and "garbage" (Nelson 1934, Marquiss and Booth 1986, Engel and Young 1989). Ravens also capture insects, reptiles, amphibians, fish, small mammals, and other birds (Marr and Knight 1982, Camp et al. 1993). I here describe a raven removing fat from a chunk of suet in an unusual or aberrant way that differs markedly from the method used by jays, crows, and most other ravens.

Chunks of beef suet that were either of sufficient size so that they could not be carried off or that were nailed onto the frozen ground

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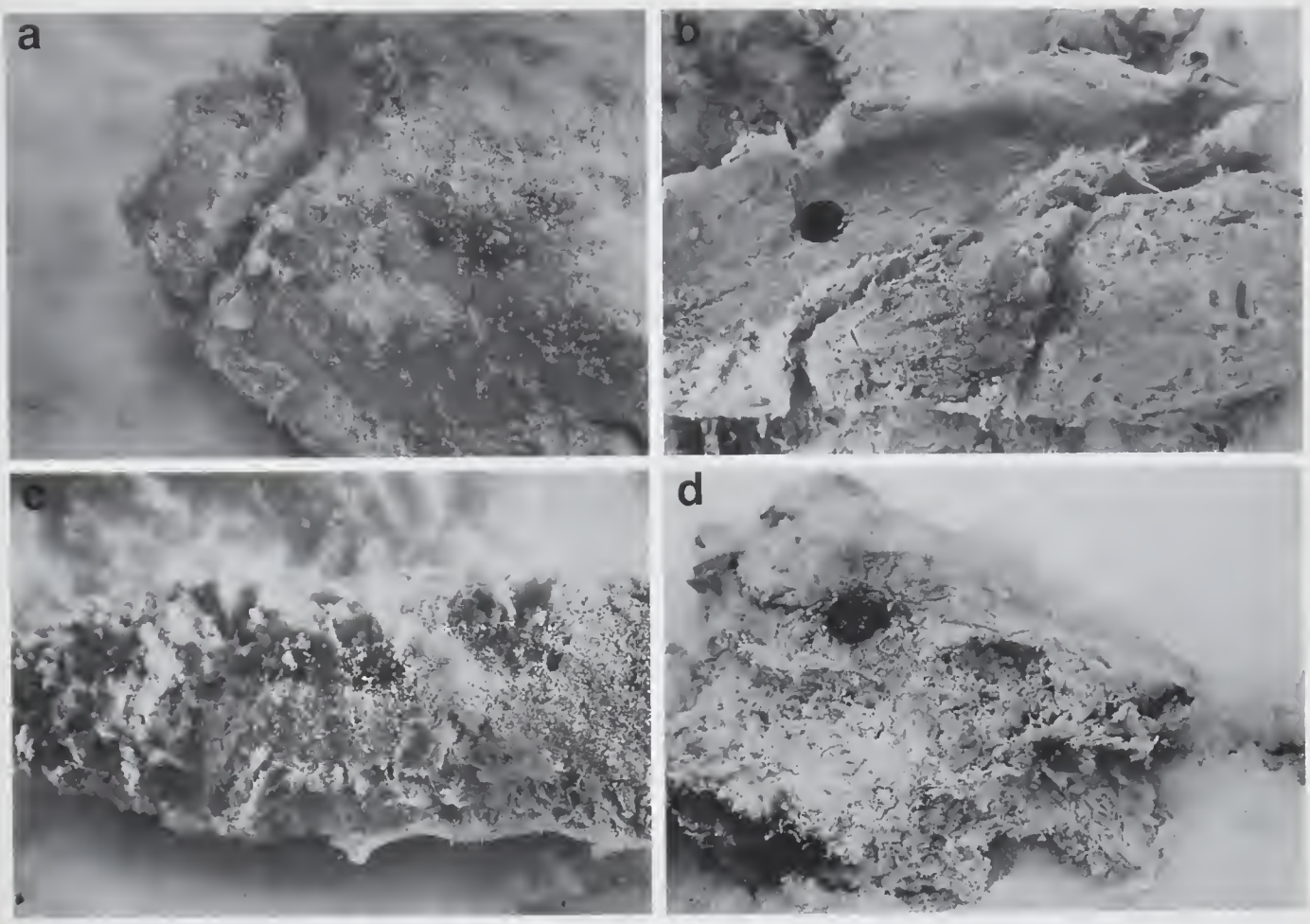

FIG. 1. Two top photographs show grooves left by ravens in suet when they were interrupted while feeding in the wild. A: Deep (1–2 cm) groove in a clear block of beef suet. B: Two grooves cut into suet adhering to ribs. C: Typical pecking pattern in suet by American Crow. D: Typical pecking pattern in suet by a Blue Jay. (Right two pictures show heads of spikes used to secure the suet onto frozen ground so that it could not be carried off.)

were provided in the forest near Hinesburg, Vermont. For many years the following species fed on suet at this site: American Crows (*Corvus brachyrhynchos*), Blue Jays (*Cyanocitta cristata*), Hairy (*Picoides villosus*) and Downy woodpeckers (*Picoides pubescens*), Black-capped Chickadees (*Poecile atricapillus*) and White-breasted Nuthatches (*Sitta carolinensis*). All of these birds fed on suet by picking into it and/or taking the most prominently protruding pieces.

On one occasion a raven flew away from the feeding station as I approached, and the pattern of pecks the raven had left on the suet was distinctive (Fig. 1A). The raven had carved a 7.5 cm long (and 1–2 cm deep) groove. I presume that I had interrupted the bird just before it had finished the task of cutting a smaller chunk of suet off the larger. The same chunk of suet had what appeared to be a pattern of a previous parallel cut (2–3 cm anterior to the unfinished cut) where the bird had already removed one slice of fat. The readily available small pieces of frozen suet chips (2–3 mm) that had been loosened were next to the groove (Fig. 1A).

When I interrupted two ravens as they were feeding on the suet at the same site on three later occasions, I found similar grooves and only raven tracks around this suet. When I left suet that was firmly attached to ribs, the ravens cut grooves through the fat down to the bone underlying the fat. No suet chunks could be removed, but the bird(s) then cut another, parallel groove (Fig. 1B). Crows and Blue Jays whose feeding patterns were observed routinely at the same site always left only peck-marks, never grooves (Fig. 1C, D). At no time have I observed groove cutting in caged ravens that I watched routinely. Neither have I seen such behavior in hundreds of

hours of watching groups of ravens feeding on frozen muscle meat in the wild.

What accounts for the ravens' unique feeding patterns on suet? The peck marks were clearly aligned in rows. Each peck could have provided only a small immediate reward, but it made possible the removal of a large chunk of fat and hence a large reward later. Since loose "crumbs" of fat were left (Fig. 1A), the delayed (greater) reward was apparently of more importance to the birds than the small proximate reward. Ravens exhibit similar apparent foresight during some aspects of their caching behavior (Heinrich and Pepper 1998).

Food access behavior is of interest because it has traditionally provided a tool for examining cognition. Examples with corvids include studies of memory (Balda and Kamil 1989, Kamil and Balda 1985, Bednekoff et. al. 1997), tool use (Hunt 1996), optimal foraging (Zach 1979, Waite and Ydenberg 1994), and insight learning (Heinrich 1995).

The fat cutting behavior is probably very rare in ravens and it is not likely an innate or hard-wired response. Therefore, the raven could have had insight of how to remove a large chunk of food for storage and/or later consumption.

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Pairing Success of Wood Thrushes in a Fragmented Agricultural Landscape

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ABSTRACT.—Habitat fragmentation has been associated with low pairing success of some Neotropical migrant songbirds occupying forest fragments. From 1996 to 1998, we conducted a nest study of Wood Thrushes (*Hylocichla mustelina*) in 21 woodlots ranging in size from 3–12 ha in a highly fragmented agricultural landscape in southwestern Ontario. We found active nests for 46 of 48 singing Wood Thrushes that we detected in the forest fragments. Our results suggest that in at least some highly fragmented agricultural landscapes, most singing Wood Thrushes in small woodlots are successfully paired. *Received 17 Sept. 1998, accepted 18 Jan. 1999.*

Habitat fragmentation has been associated with low pairing success of some Neotropical migrant songbirds residing in forest fragments and along forest edges. For example, fewer territorial male Ovenbirds (*Seiurus aurocapillus*) were paired in small forests than in large ones in Missouri (Gibbs and Faaborg 1990, Van Horn et al. 1995), New Jersey (Wander 1985), Ontario (Burke and Nol 1998), and Québec (Villard et al. 1993). Ziehmer (1993, cited in Faaborg et al. 1995) documented lower pairing success for Red-eyed Vireos (*Vireo olivaceus*) and Wood Thrushes (*Hylocichla mustelina*) around clearings in large, selectively logged forests in Missouri.

With respect to Wood Thrushes, diminished pairing success may not apply generally across all fragmented landscapes. We report on high pairing success of Wood Thrushes in forest fragments in Waterloo Region, an intensively farmed landscape with 14% forest cover and where the mean patch size of woodlots was 12.8 ha (± 18.3 SD). (See Friesen et al., 1999 for a fuller description of the regional landscape.)

From 1996 to 1998, as part of a larger regional study on nesting success and productivity of several species of forest birds (Friesen et al. 1999), nest searches were conducted in 21 woodlots known to hold Wood Thrushes; woodlot size ranged from 3–12 ha ($\bar{x}$ = 8.2 ± 3.3). The canopy at all sites, which averaged 24 m in height, was dominated by sugar maple (*Acer saccharum*) and smaller amounts of white ash (*Fraxinus americana*) and American beech (*Fagus grandifolia*). Maple and ash saplings, alternate-leaved dogwood (*Cornus alternifolia*), and red-berried elder (*Sambucus pubens*) predominated in the openings created by ongoing and recent selective logging at all sites.

Searches for singing males involved four to eight early morning visits to each site beginning the last week of May and continuing to 20 June. We located and mapped the location of all singing birds at each woodlot by walking parallel transects 100 m apart and using taped song playbacks (Yahner and Ross 1995). We attempted to find nests for all singing birds using four- and five-person teams. Nest searching, conducted within a 200 m radius of the singing bird, was discontinued if an active nest (i.e., containing eggs or young) was not found within 15 person hours. Singing birds were assumed to be paired if an active nest was found in their vicinity.

Although many singing birds were detected after 20 June, less effort was expended in finding their nests because of the time constraints involved in monitoring the nests found previously. In addition, first broods in southern Ontario generally fledge around 20 June (Friesen, Wyatt, and Cadman, unpubl. data) and singing birds encountered thereafter could have been unpaired males moving about between nests or they could have become unpaired following the failure of earlier nests (Roth and Johnson 1993). We were less confident of locating all territories later in the breeding season because birds were then less

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likely to respond to taped playbacks (Friesen, Wyatt, and Cadman, pers. obs.). Consequently, data collected after 20 June were not included in this analysis.

One to three singing males were found in each woodlot, with 48 territorial birds detected overall. Active nests were found for 46 (96%) of the singing Wood Thrushes, with 2.0 (± 1.7) person hours expended on average to find each nest following the detection of a singing bird. Nest height averaged 3.1 m (± 1.5 m, range 1.2–6.4 m). Our estimate of pairing success may be conservative because a new but empty nest was found in the vicinity of one of the two "unpaired" singing males (suggesting recent predation) and it is possible that we missed finding the nest of the other "unpaired" male.

Although Neotropical migrants can experience poor pairing success in fragmented habitats, sensitivity in this regard likely varies among species. Based on their pairing success in small fragments, Ovenbirds seem to be particularly sensitive to fragmentation effects while Wood Thrushes are less so. Burke and Nol (1998) speculated that the lower pairing success of Ovenbirds in small forests might be attributed to the absence of females who avoid these areas of lower food abundance in favor of larger forests. Wood Thrushes, but not Ovenbirds, commonly inhabit small rural woodlots in our study area (Friesen et al. 1995). As both species are ground foragers dependent upon similar types of prey (Kaufman 1996), it may be that factors other than food availability or perhaps subtle differences in food preferences are limiting the distribution of Ovenbirds in our region.

It may be, too, that a species' pairing success varies across regions, perhaps in response to factors such as differences in landscape configuration, forest structure, disturbance regimes, and population density. In Missouri, where Wood Thrushes are "forest interior" species that only occasionally occupy small woodlots (Jacobs and Wilson 1997), lower pairing success occurred as formerly continuous forest became fragmented by logging activities (Ziehmer 1993, cited by Faaborg et al. 1995). In our highly fragmented landscape, Wood Thrushes exhibit a high level of pairing success. Weinberg and Roth (1998) did not explicitly comment on the pairing success of Wood Thrushes in their study in Delaware; however, based on the large number of active nests (120 over two years) they found in 14 forest fragments ranging in size from 0.2–2.1 ha, it appears that Wood Thrush experience a high degree of pairing success in other fragmented landscapes as well.

Our findings on pairing success do not necessarily imply that Wood Thrushes in southwestern Ontario are immune to fragmentation pressures. For example, almost half of the Wood Thrush nests found in Waterloo Region in 1996 and 1997 were parasitized by Brown-headed Cowbirds (*Molothrus ater*) resulting in a significant decline in host productivity (Friesen et al. 1999). With respect to mating status, however, our data strongly suggest that most singing males detected in forest fragments early in the breeding season are likely to be paired.

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Connecticut Warbler, a North American Migrant New to Ecuador

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ABSTRACT.—We present the first record of the Connecticut Warbler (*Oporornis agilis*) for Ecuador. The bird was mist-netted and photographed on 21 November 1996 at Playa de Oro, Rio Santiago, Esmeraldas Province, northwestern Ecuador. *Received 15 Sept. 1998, accepted 14 Nov. 1998.*

Between August 1995 and December 1996, we studied understory bird communities near the village Playa de Oro (00° 52′ N, 78° 47′ W) situated at about 50 m above sea-level on the Río Santiago, Esmeraldas Province, northwestern Ecuador. Since February 1997 we have carried out line transect censuses in different habitat types from 50 m to 400 m in the community of Playa de Oro, close to the border of the Cotocachi-Cayapas ecological reserve. On the morning of 21 November 1996, a warbler of the genus *Oporornis* was mist-netted in secondary vegetation near a natural backwater pond on the outskirts of Playa de Oro. The bird had a complete, pale, whitish-yellow eye ring, very long undertail coverts, a dull brown breast band encircling a paler throat, a grayish tinged hood and grayish legs (Fig. 1). Referring to the description in Curson and coworkers (1994), we determined that the bird was a first winter Connecticut Warbler (*Oporornis agilis*). Its measurements were: total length (non-stretched) 125 mm, wing 65 mm, tail 43 mm, wing − tail 22 mm, bill length 11.95 mm, tarsus 19.65 mm, body mass 12.5 g. P7 and p8 were emarginated. After the bird was photographed in different positions (upperparts, underparts, laterally, and with opened wing) it was released. The photographs of the wing formula (primaries) show p9 longer than p6. The difference was not measured exactly in the field. Because a few female and immature *O. philadelphia* also have complete eye rings, it was necessary to verify the identification using wing and tail measurements. According to Lanyon and Bull (1967), *O. agilis* can usually be separated from *O. philadelphia* by a wing − tail value equal to 19 mm or more. The bird we captured showed a wing − tail value of 22 mm, hence its identification as *O. agilis* is virtually certain. Photos have been deposited at VIREO, where the identity as *O. agilis* has been confirmed by L. Bevier and R. S. Ridgely (pers. comm.), Academy of Natural Sciences, Philadelphia.

Oporornis agilis is a rare to locally uncom-

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FIG. 1. Connecticut Warbler, *Oporornis agilis*, captured at Playa de Oro, Esmeraldas Province, northwestern Ecuador.

mon boreal winter resident south and east of the Andes, from eastern Colombia and Venezuela south to eastern Peru, northern Bolivia and west central Brazil (Curson et al. 1994, Ridgely and Tudor 1989). Recent evidence (R. S. Ridgley, pers. comm.) indicates that the species occurs in the northern part of South America mainly as a transient, but not during the northern mid-winter months. The bird trapped in Playa de Oro apparently represents not only the first record of *O. agilis* west of the Andes but also the first record from anywhere in Ecuador (R. S. Ridgely, pers. comm.), although it had been expected in that country.

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Parental Behavior of a Bigamous Male Northern Cardinal

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ABSTRACT.—Parental behavior of a bigamous male Northern Cardinal (*Cardinalis cardinalis*) in southwestern Ohio in 1997 is described. The male was neither brighter in plumage nor larger than average. Nesting periods of the two females overlapped. The male provisioned the primary female during incubation but not the secondary female. The male delayed provisioning the secondary female's nestlings until two days after they hatched but then fed both sets of nestlings at rates typical of monogamous males. Despite initially reduced paternal care, the brood of the secondary female fledged successfully. *Received 12 Mar. 1998, accepted 15 Nov. 1998.*

The majority of bird species are socially monogamous (Lack 1968), the hypothesis being that ecological constraints explain the relative infrequency of polygyny in birds (Emlen and Oring 1977). At the same time, males in most species of socially monogamous birds may have the behavioral capability of becoming polygynous should ecological conditions allow multiple mates (Smith et al. 1982, Wingfield 1984). The description of infrequent cases of bigamy in socially monogamous species is relevant to any discussion of intraspecific variability in mating arrangements. The behavior of bigamous males toward two females and their offspring may provide information on the costs to females involved in such mating arrangements.

Northern Cardinals (*Cardinalis cardinalis*) are socially monogamous and sexually dichromatic; the parental behavior of bigamous males has not been previously described in detail. Here, we document bigamy and paternal care by a male Northern Cardinal observed during 20 h over a 10 day period in early June 1997.

The three cardinals, all of unknown age, were members of a color-banded population located at Aullwood Audubon Center, 15 km northwest of Dayton, Ohio (39° 52′ N, 84° 16′ W) and under continuous observation since 1991. The 80 ha property is a mixture of deciduous woodlands, meadows, and prairies where cardinals are abundant. The male that became bigamous in 1997 was banded in the spring of 1996. That year he was successful over several others competing for a territory that had been occupied for several years by a male that disappeared over the 1995–1996 winter. The territory was one of the largest in the study area and among those with the most plant cover, a variable that might provide an advantage to nesting success (Conner et al. 1986, Wolfenbarger 1996; however, see Filliater et al. 1994). The male enlarged this territory in 1997 and it became the site of the bigamous mating.

One of the two females paired with this male in 1997 (♀ 650) was banded in 1996 on a territory adjacent to the one he occupied in 1996. This female's mate disappeared in the non-breeding season 1996–1997, as did the mate of the [bigamous] male. Female 650 remained on the same territory in 1997 and the bigamous male expanded his 1996 territory to include the area occupied by female 650. In 1997, this female was treated differently by the male from the manner in which females of monogamous males are treated by their mates (described below), and for these reasons we consider her the "secondary" female of the bigamous male. The other female (♀ 555) had been banded two years previously in an area two territories away from the bigamous male's 1996–1997 territory. She mated in 1995 but was not found in 1996; her 1995 mate retained the same territory in 1996 and mated with another female. Female 555 then reappeared in 1997 on the territory from which the bigamous male's 1996 mate had disappeared. The bigamous male treated female 555 similarly to how monogamous

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males treat their mates, and we consider her the "primary" mate of the bigamous male. We do not know which female first associated with the bigamous male in 1997.

Male cardinals provision their mates during courtship, egg-laying, and incubation (Lemon 1968; Verner and Willson 1969; Breitwisch, Banks, Donahoo, LeClair, and Schilling, unpubl. data); this is considered a form of indirect parental care (Lyon and Montgomerie 1985). We sampled provisioning behavior of the bigamous male toward both females during six 1-h observations on six days of the 12-d incubation period. The nests, located approximately 60 m apart and out of sight of each other, were monitored simultaneously during these observation periods, which included both mornings and afternoons. Neither age of eggs nor time of day influences rate of mate provisioning by male cardinals (Breitwisch, Banks, Donahoo, LeClair, and Schilling, unpubl. data). Primary female 555 began nesting a few days before secondary female 650, and the bigamous male provisioned female 555 at a similar rate ($\bar{x}$ = 1.00 feeding/h) to the mean value for the monogamous population [$\bar{x}$ = 1.05 ± 0.48 (SD) feeding/h; Breitwisch, Banks, Donahoo, LeClair, and Schilling, unpubl. data]. However, female 650 received no food from the bigamous male. This is in marked contrast to a sample of 18 monogamous males in the population, all of which provisioned their mates during incubation (Breitwisch, Banks, Donahoo, LeClair, and Schilling, unpubl. data). Although the bigamous male did not provision female 650, he remained active throughout his territory and did not appear to favor the area near the nest of female 555.

Male cardinals feed nestlings at high rates, frequently surpassing the rate at which females feed nestlings (Filliater and Breitwisch 1997, Linville et al. 1998). We sampled nestling feedings by the bigamous male and the two females during 1-h samples on seven days at female 555's nest and six days at female 650's nest. Sampling periods on four of the days were coincident (see below). Observation periods included mornings and afternoons, although Filliater-Lee (1992) showed that neither male nor female feeding rate is related to time of day. The eggs of female 555 hatched three days before the eggs of female 650. The male fed the two nestlings of female 555 at a mean rate of 1.3 feeding/nestling/h, similar to the feeding rate by monogamous males ($\bar{x}$ = 1.1 ± 0.53 feeding/nestling/h; Filliater and Breitwisch 1997). Female 555 fed her nestlings at a mean rate of 0.57 feeding/nestling/h, similar to the feeding rate by females mated to monogamous males ($\bar{x}$ = 0.87 ± 0.38; Filliater and Breitwisch 1997). However, the male did not begin feeding the two nestlings of female 650 until two days after they hatched. Female 650 fed her nestlings at a mean rate of 1.0 feeding/nestling/h, similar to that of females mated to monogamous males. When the male began to feed female 650's nestlings, he fed them at a mean rate of 1.0 feeding/nestling/h, similar to the rate of feeding by monogamous males. During four days, nestlings were present in both nests and the male fed nestlings at both, roughly alternating his deliveries to the two sets of nestlings.

The fates of these two nests differed. The nestlings of the primary female were preyed upon a few days before they would have fledged, but the nestlings of the secondary female fledged successfully. We do not know whether the three adults maintained the bigamous relationship throughout the season.

We determined that the bigamous male was neither exceptionally ornamented nor notably large in body size. Using a technique described by Linville and coworkers (1998), we measured the brightness of the red breast plumage of the male and of the red underwing plumage of the two females. The bigamous male and one other male were tied as the dullest in a sample of 14 males in 1997. The bigamous male was also of average body size, as measured by both tarsus and flattened wing arc (R. Breitwisch and S.U. Linville, unpubl. data). The females were both found to be at least equal to the median plumage brightness of 15 females in 1997. Primary female 555 was one score lower in brightness than secondary female 650. We lack size measurements of the two females.

Our observations suggest that there are at least potential costs for a secondary female mated to a bigamous male cardinal. Most dramatically, the bigamous male failed to provision the secondary female during incubation. A monogamous male typically provides ap-

proximately 150 feedings at the nest during the 12-d incubation period and probably supplies the female with a significant amount of food away from the nest (Breitwisch, Banks, Donahoo, LeClair, and Schilling, unpubl. data). The high rate of mate provisioning indicates that the amount of food provided may be important to the female's nutritional state, especially when considering the three or more clutches of eggs laid by a typical female in this population during a breeding season (Filliater et al. 1994). The bigamous male's behavior toward the secondary female's nestlings was not typical of monogamous males in this population. Although the male eventually began to feed the nestlings and did so at a rate typical for monogamous males, he delayed two days after these nestlings hatched before beginning to feed them.

The primary contribution of male cardinals to raising young appears to be provisioning the female, nestlings, and fledglings. Guarding and active defense against predators are of minor importance and effectiveness (Filliater et al. 1994, Nealen and Breitwisch 1997). Thus, we think it unlikely that any reduced level of these components of paternal care were a significant additional cost of bigamy to either female.

Bigamy in cardinals appears to be quite rare (see Linville and Halkin, in press). Lemon (1968) observed two cases in which he noted that the females "less tended" by the bigamous males eventually left and were probably unsuccessful (R. E. Lemon, pers. comm.). In our own studies, the instance of bigamy described here is the first witnessed in seven years of monitoring mating relationships in this population. Each of the last six years, we have observed an average of about 20 territories, suggesting that the incidence of bigamy is probably less than 5% [Verner and Willson's (1969) criterion for monogamy] and may be even less than 1%. Two other researchers have not observed bigamy in multiyear studies with a combined sample size of more than 50 pairs (G. Ritchison, pers. comm.; L. L. Wolfenbarger, pers. comm.). D. M. Scott (pers. comm.) and R. E. Lemon (1957, 1968, pers. comm.) have records of at least three bigamous males in multi-year studies of more than 50 pairs of cardinals, although Scott (pers. comm.) agrees with the above estimate of less than a 5% incidence.

It has been hypothesized that staggered timing of nesting by two females mated to a bigamous male may be critical to reducing the cost of bigamy to the females (Verner 1964, Breitwisch et al. 1986, Derrickson 1989). Bigamous males should be able to apportion care more easily when nests do not overlap in time. Obviously, we cannot know if the bigamous cardinal would have provisioned the secondary female if her incubation period had not overlapped with that of the primary female. Second, with staggered nesting, a female occupied with caring for eggs or nestlings might display reduced aggression toward a second female attempting to nest (Derrickson 1989). Although female cardinals can be very aggressive toward other females (R. Breitwisch, pers. obs.), we did not witness aggression between the two females we observed.

In any case, the secondary female cardinal was successful in producing fledglings despite limited paternal care. Richmond (1978) removed male cardinals from nesting pairs and also found that females were able to raise young by themselves. We speculate, as did Richmond, that neglected females may still pay a cost in future survival from such high parental effort.

The question that remains is whether a secondary female in a bigamous relationship is making the correct decision at the time of pairing with a male or committing an error. It seems likely that there is no single answer to this question. In some monogamous species, secondary females may be able to "predict" that their young will receive paternal provisioning [e.g., Northern Shrikes, *Lanius excubitor,* and Loggerhead Shrikes, *L. ludovicianus,* (Yosef 1992)]. In others, lack of paternal provisioning may be equally predictable [e.g., Song Sparrows, *Melospiza melodia* (Smith et al. 1982), Florida Scrub Jays, *Aphelocoma c. coerulescens* (Woolfenden 1976)], or paternal provisioning may depend on degree of overlap in nesting [e.g., Northern Mockingbirds, *Mimus polyglottos* (Logan and Rulli 1981, Breitwisch et al. 1986)]. Moreover, there are other factors that may be involved in determining level of paternal care at nests of secondary females, both in species that are opportunistically bigamous and those that are typically

more polygynous. These include the degree to which an aspect of paternal care is shareable, the age and number of nestlings, and the male's confidence of paternity (Searcy and Yasukawa 1995). Explanations of such varied patterns will await additional reports on bigamous relationships in socially monogamous birds.

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Special Report

A SURVEY OF UNDERGRADUATE ORNITHOLOGY COURSES IN NORTH AMERICA

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ABSTRACT.—The Committee on Undergraduate Education of the Wilson Ornithological Society conducted a survey of ornithology courses in North America as a service for teachers of ornithology. Our survey of 26 responses uncovered 26 creative approaches to teaching ornithology. Nonetheless, a number of commonalities exist. Courses at small colleges and large universities include both lecture and laboratory components and usually extend into the spring. Most courses emphasize anatomy and physiology, nesting, evolution of birds, ecology, and flight, with other topics receiving few or no lectures. Almost 60% of the courses include student dissection or faculty demonstration. Some courses use preserved birds, others use birds that died accidentally, and one uses roasted chickens that are eaten as part of the skeleto-muscular dissection. Laboratory sessions emphasize taxonomy and identification of local and, often, world birds. Most schools have at least a small collection of specimens available for student use. Courses usually include an extensive project and written work. We hope the results of the survey will stimulate discussion among teachers of ornithology as we seek to develop new ideas for our courses. *Received 29 Sept. 1997, accepted 8 Jan. 1999.*

The Wilson Ornithological Society's Committee on Undergraduate Education seeks to increase the quality of teaching of ornithology at the undergraduate level and to foster communication among ornithology teachers about successful and unsuccessful aspects of their courses. With these goals in mind, we prepared a questionnaire that was sent to all ornithology faculty who responded to a request printed in the Ornithological Societies of North America newsletter. The following is a synthesis of the information provided by the 26 ornithologists who completed the questionnaire in 1993 and 1994. Some respondents left one or more questions unanswered, thus our analysis of some questions is based on fewer than 26 responses.

The questionnaire included demographic and course content questions. Copies of all completed responses are available from the Van Tyne Library at the University of Michigan. We first describe the demographics of our sample, then summarize the quantitative data, and close with a discussion of successful and unsuccessful aspects of the courses.

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DEMOGRAPHICS OF THE RESPONDENTS' INSTITUTIONS

Our small sample is not amenable to multivariate analysis. Furthermore, because it is based on only 26 respondents, our survey may be biased. Our intent is to document the diversity of approaches and stimulate discussion.

The 26 responses to the survey came from ornithology teachers in 18 states and 1 Canadian province. Thirteen of the respondents teach at schools in the Eastern Time zone, 11 at schools in the Central Time zone, and 2 in schools in the Mountain Time zone. We received no data from faculty teaching at schools in the Western Time zone. Of the 24 schools in the Eastern and Central Time zones, 5 are in southern states. Fifteen of the colleges and universities are located in small towns, whereas 11 have suburban or urban campuses. Sixteen of the respondents teach at state-supported, public institutions; 7 teach at privately supported, non-denominational colleges or universities; and 3 teach at church-affiliated colleges. Twelve of the schools offer the Ph.D., 4 the M.Sc. as their highest degree, and the remaining 10 offer only bachelors' degrees. Twelve schools have more than 10,000 undergraduates, hereafter referred to as large schools, and 14 schools have fewer than 10,000 (small schools); 7 of these have 2,000 or fewer.

TABLE 1. Quantitative comparison of enrollment as affected by prerequisites for ornithology courses taught at large and small schools.

Prerequisites	Large schools (>10,000)		Small schools (≤10,000)	
	No. of schools	Mean class size (±SD) (1988–1993)	No. of schools	Mean class size (±SD) 1988–1993)
None	1	50.8 ± 6.8	2	21.3 ± 2.7
1 semester biology	7	30.9 ± 20.0	8	12.6 ± 4.5
2+ semesters biology	4	26.6 ± 25.7	4	17.0 ± 12.5
Overall class size	12	31.4 ± 21.7	14	14.9 ± 8.1

THE COURSE

Goals.—The generally stated goal of the classroom portion of the course was to provide students with a broad overview of ornithology, and to use birds as examples of fundamental concepts of biology and, to a lesser extent, cognate disciplines. A second goal was to use birds to illustrate the scientific process, which includes hypothesis testing and stimulation of new ideas through debate between scientists with different interpretations of the data. A third goal, emphasized by three respondents, was to build a genuine admiration of the many adaptations of birds, thereby promoting the life-long study and enjoyment of birds.

Goals for the laboratory portion of the course were more varied. Most faculty saw field identification by sight and song as a primary goal. Family and order names were considered part of identification by most respondents. Providing students with a working knowledge of topography and anatomy, particularly of feathers, was another common goal. Six respondents sought to instill appreciation of behavior and ecology through field experiences. Another six respondents indicated that a goal of the laboratory was to introduce students to field (e.g., banding, censusing, recording of vocalizations, etc.) or museum (e.g., preparation and measurement of study skins) techniques.

Structure.—One semester of introductory biology or zoology was a common prerequisite although no prerequisite and two or more prerequisites also occurred. Class size varied significantly with the number of prerequisites at both large ($F_{2, 53} = 4.71$, $P < 0.05$) and small ($F_{2, 49} = 4.05$, $P < 0.05$) colleges and universities (Table 1). Ornithology classes with a single prerequisite had smaller enrollments in schools of both sizes (large: $t = 3.78$, df = 38, $P < 0.001$; small: $t = 3.74$, df = 35, $P < 0.001$) than courses with no prerequisite. Enrollment did not decline further with a second or third prerequisite (Table 1). Overall, class size at small schools was significantly less ($t = -5.67$, df = 106, $P < 0.001$) than at large schools (Table 1).

Faculty at large schools were more likely ($\chi^2 = 6.09$, df = 1, $P < 0.05$) to offer ornithology annually than those at small schools, but the duration of the courses varied similarly among schools of different sizes (Table 2). All but three of the courses were taught in the

TABLE 2. Quantitative comparison of some characteristics of ornithology courses taught at large and small schools (based on number of students enrolled).

Characteristics	Large schools (>10,000)	Small schools (≤10,000)
Frequency		
Annually	10	5
Biannually	2	8
2–3 yr interval	0	1
Duration		
14–16 wks	10	11
13 wks	1	1
10 wks	0	1
7–8 wks	1	1
Lecture h/wk		
4	0	1
3	3	10
2	7	3
1	1	0
Use of primary literature		
Assigned to students	6	10
Not assigned to students	6	4
Labs/wk/student		
0	1	0
1	6	11
2	4	3
3	1	0

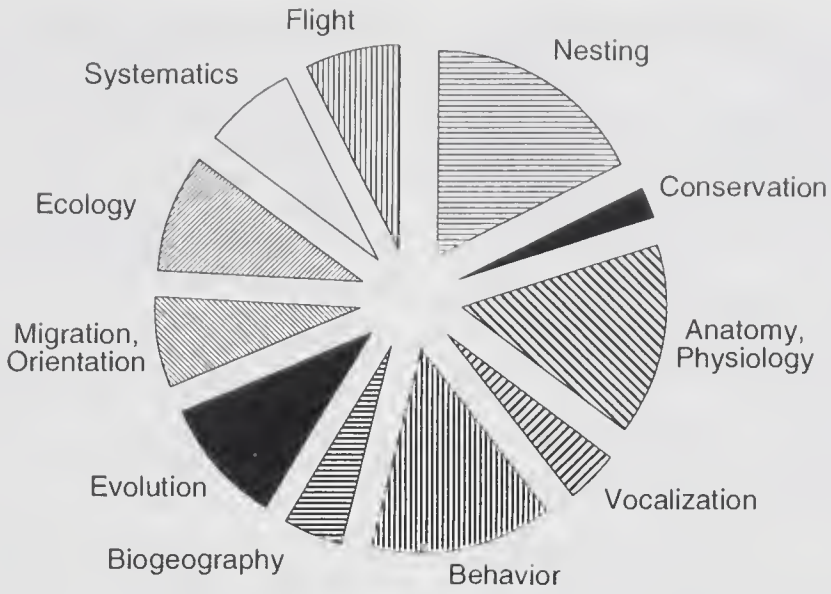

FIG. 1. The proportion of the "consensus" ornithology course devoted to the subjects indicated.

spring semester beginning in January when students learn to identify waterfowl, raptors, and relatively few winter residents. Later in the course, as their field skills improve, students are exposed to an increasing diversity of spring migrants and summer residents.

Twenty-four courses included both lecture-discussion and laboratory. Lecture-discussion sections met twice weekly for 75 min/meeting in 12 courses, three times/week for 50 min/meeting in 8 courses, and as 1 three-hour seminar in 3 courses. Faculty at small schools provided more hours of lecture-discussion/week ($\chi^2 = 6.75$, df = 1, $P < 0.01$, Table 2) than those at large schools. Faculty expressed satisfaction with the longer class period and with occasions when lecture and laboratory could be integrated.

The typical class period was what one respondent characterized as a "loose lecture," a mix of lecture and discussion, illustrated with specimens, slides and video tapes, and punctuated with questions from the teacher. Several faculty indicated plans to incorporate software in the future, but none were using computers in the classroom in 1993 and 1994 when the survey was completed.

Content.—Two courses used only the primary literature, 24 courses required texts, 9 of these required two texts, and 1 required three. Gill's (1990; the survey was completed just before the second edition) Ornithology was the preferred text by a wide margin (Appendix), but other texts were used. In addition to a text, 15 respondents assigned their students readings from the primary literature. No difference in use of the primary literature was evident among schools of different sizes (Table 2).

Each respondent was asked to provide a syllabus of his or her course. We assigned the lectures to 11 broadly defined topics. The mean proportion devoted to each topic by all respondents is shown in Fig. 1. Some error was unavoidable as we tried to categorize lectures into the eleven topics. Nevertheless, this figure represents the "consensus" course of the surveyed teachers.

Most courses had one laboratory session/student/week (Table 2) and in most courses it was a mix of indoor and outdoor sessions. Laboratory schedules were similar at large and small schools (Table 2).

Nineteen courses devoted one or more laboratories to dissection of birds. Of these, two courses had demonstration dissections by faculty only. Eight faculty provided their own dissection guide (Appendix), but others relied on Pettingill (1990) or Faaborg and Chaplin (1988b). Preserved pigeons (*Columba livia*) were used for dissection by 13 of 19 respondents. One person used fresh pigeons. Chickens (*Gallus gallus*), Japanese Quail (*Coturnix coturnix*), European Starlings (*Sturnus vulgaris*), House Sparrows (*Passer domesticus*), and birds killed in accidents were used in the remaining courses or for comparison with pigeons. One ornithologist brought a roasted

chicken to laboratory for dissection and subsequent consumption.

Most instructors required students to own a field guide. The appropriate Peterson guide [eastern (1980) or western (1984) North America] was the most popular choice (Appendix).

Twenty-three of 25 respondents who taught a course with a laboratory component required students to learn to identify species of birds by sight, usually of the local avifauna. The number of birds students had to learn varied from fewer than 50 to over 200, with 101–150 being typical.

Seventeen of the 23 also required their students to learn to identify some birds by song. The number of species each student had to learn ranged from 21 to 100 with 41–60 being typical. To help students learn vocalizations, respondents identified the Peterson tapes, the Birding by Ear tapes, and the National Geographic Society tapes as particularly useful. One respondent had prepared an audiotape specific to the birds that students had to learn in the course. A few respondents taped songs with students and had the students analyze the songs themselves. This not only taught students recording and analytical techniques, but also gave them a thorough knowledge of the characteristics of the songs they recorded. To test students' abilities to identify birds by sight and sound, 87% of the respondents gave laboratory examinations and 35% gave examinations in the field.

The amount of taxonomy students had to learn varied. Twenty of 25 instructors required students to learn order names and know the distinguishing features of each order. Family names were required for students in 16 of the courses. Few instructors required that genera (two courses) and species (one course) names be learned.

Most courses required a long written report, and a few also required one or more short written assignments. Long written assignments included the following:

- detailed field journal based on 20 hours or more of fieldwork in addition to the regular laboratory field trips;
- term paper based on original field or laboratory research or a literature review covering some aspect of avian biology;
- joint paper by several students working on limited and local research topics. The teacher did the literature search. The students added their own data and synthesized the material;
- paper based on observations of a bluebird box on campus. Students monitored the assigned box from late March until the young fledged;
- paper based on the social behavior of a particular species with monitoring of the species over the course of the semester;
- research paper that usually involved field research, data analysis, and literature review in which the teacher and classmates reviewed a rough draft before the final draft was submitted;
- paper based on field research on the behavior, ecology, or migration of a local bird species. One instructor disallowed references to encourage the creativity and the observational and analytical skills of each student;
- paper based on a census of the birds of a site that has been censused annually since 1971;
- an account of a local bird in the style used by the Birds of North America;
- paper based on the analysis of a large sample of banding data for Yellow Warblers (*Dendroica petechia*). The students could analyze site fidelity as a function of age and sex, arrival dates as a function of age and sex, etc.;
- analysis of the population dynamics of a species based on Christmas Bird Count data.

Short written assignments included the following:

- one page summary of a published article;
- computer spreadsheet assignments on energetics of flight and thermoregulation;
- three critiques of a set of three or four papers with contradictory views on a particular issue. Each student summarized each paper and then offered critical comment on each, taking a position on one side of the controversy;
- weekly 5–10 minute essays written in class on specific ornithological questions;
- two critiques of recent ornithological articles written in the format of the Recent Literature section of the Journal of Field Or-

nithology. The critiques had to be rewritten until they reach "A" quality.

SUPPORT FOR UNDERGRADUATE ORNTIHOLOGY

Avian specimens were equally available to respondents at large and small schools. Faculty used collections to illustrate taxonomic principles, avian systematics, and less often to illustrate morphological, ecological, and behavioral adaptations. In five courses, students were required to prepare one or more study skins. Skin preparation was optional in six other courses.

Collections available at small and large schools were similar in size with 9 of 23 collections having fewer than 1,000 specimens, some with fewer than 300. Eighteen of the 23 collections had a regional focus, two had broad North American representation, and three had large collections representing birds of the world. All collections included study skins, most included mounts and skeletons, and some included eggs, nests, and alcoholic specimens.

Fifteen schools owned some of the natural areas visited by the class. Use of these areas varied from carefully scheduled, multi-year censusing of an arboretum managed by the university, to intermittent visits to unmanaged areas for "birding." Here as with use of museum collections, faculty might benefit from sharing ideas on how university-owned natural areas could be used in conjunction with an ornithology course.

MOST SUCCESSFUL PARTS OF THE COURSE

Respondents were asked to describe the most successful parts of their courses. Fifteen listed some aspect of field trips as the most successful portion of the course. Interestingly, one respondent found that some students loved the laboratory/field portion of the course while others hated it. Listed below are the teaching aids and activities instructors found most successful:

- audiotapes and CDs of bird songs to facilitate vocal identification of birds;
- breakfast with the class before or after morning field trips;
- color slides, whether the instructor's own or supplemented from VIREO. One instructor provided detailed notes on each slide so that students could devote full attention to the slides;
- demonstration or experiment that gets students involved in active learning;
- field trips to build enthusiasm for learning species identification and understanding the biology of birds;
- laboratory and lecture sessions on the same day to encourage integration of the material;
- lectures on ecology and behavior;
- list of mnemonic devices generated by students for learning vocalizations;
- lecture demonstrations, for example use of parachutes, gliders, ornithopters, and mounted wings in a wind tunnel to illustrate principles of flight;
- mist-netting and bird-banding to excite students' interest, particularly early in the course or in conjunction with ongoing research in which the students could participate;
- morphological, ecological, and behavioral adaptations of birds;
- study specimens before field trips;
- videotapes, especially those from the Nature series on Public Broadcasting: for example Marathon Bird, Rulers of the Wind, Master Builders, the Bee Team (on social behavior in White-fronted Bee-eaters), and Jewels (hummingbirds);
- use of the Macintosh software SoundEdit (MacRecorder). Annotated vocalizations of 40 species were provided on departmental hard disks. Students could play vocalizations of species they found confusing. The software also allowed students to make sonograms and spectrograms of vocalizations;
- laminated color photographs of birds to sharpen identification skills, most useful for institutions with a limited teaching collection;
- students were provided with essay questions a week in advance of the test and could return outlines of their answers at least 48 hours before the test for comments by the teacher;
- use of the "Gone Birding" game to introduce students to identification. The game helped promote the goals of enjoyment and group learning as well as improving iden-

tification skills and knowledge of species–habitat associations.

LEAST SUCCESSFUL PARTS OF THE COURSE

Each respondent was asked to identify the least successful portions of his or her course. Fellow ornithology teachers can offer little help with three common complaints: insufficient time, cold weather, and conclusion of the semester before the arrival of many spring migrants. Lecture was most often listed as the least successful part of the course. The least successful lecture topics included systematics and physiology and anatomy, despite the fact that each occupied a substantial part of the "consensus" course (Fig. 1). Additional areas that some faculty listed as least successful included using study skins to teach identification and taxonomy, using tapes to learn bird vocalizations, and teaching students field techniques, especially how to quantify behavior in the field. We hope that this list can stimulate ideas that will improve these portions of the courses.

TEACHING MATERIAL NOT PRESENTLY AVAILABLE

When asked to identify teaching aids that do not appear to be commercially available, most respondents indicated a preference for interactive software. Most would use such software to help students learn identification of birds. Specific needs are listed below. If any readers know of such aids, please notify us or a member of the Wilson Ornithological Society Committee on Undergraduate Education.

- good video, laser disk, or CD-ROM that deals only with ordinal characteristics;
- good video, laser disk, or CD-ROM that deals only with familial characteristics;
- software that illustrates the principles of taxonomy;
- video or computer disks illustrating field characteristics of birds and their vocalizations accompanied by sonograms. Such material would allow students to learn at their own pace;
- software simulations of population dynamics and evolution;
- simple, user-friendly manual on field techniques in ornithology, directed toward students.

CONCLUSION

Ornithology is part of the curriculum at large and small, public and private, graduate and undergraduate schools throughout North America. The responses to our survey confirmed our sense that ornithology is an exciting, interactive subject taught by men and women with a genuine enjoyment of birds. The desire to engender that same life-long enjoyment in others was a common theme running throughout all the responses. Beyond this common theme we were impressed with the diversity of creative ideas contained within the courses. We hope that our respondents' ideas as we have presented them will stimulate others to introduce new ideas into their ornithology courses and to bring those ideas and their reception by students to ornithological meetings for discussion by all who teach the biology of birds. Finally the Wilson Ornithological Society's Committee on Undergraduate Education would be glad to work with any ornithologist who has ideas or suggestions related to the teaching of ornithology. The Committee is eager to promote increased public discussion of teaching philosophies and ideas. We hope this paper marks the beginning of that public discussion.

ACKNOWLEDGMENTS

We thank the 26 faculty who took the time to respond to our questionnaire. We hope that we have represented their responses accurately. We thank the members of the Wilson Ornithological Society's Committee on Undergraduate Education for their suggestions throughout the development of the questionnaire and its analysis, most particularly E. J. Willoughby and L. Moseley. The manuscript benefited from the many helpful comments of K. L. Bildstein, A. J. Gatz, D. C. Radabaugh, and an anonymous referee.

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APPENDIX

Texts used for lecture, dissection, and fieldwork are listed alphabetically by author (number of courses using the text are in parentheses).

Primary lecture text: Faaborg and Chaplin 1988a (2), Gill 1990 (18), Pettingill 1990 (5), Welty and Baptista 1988 (1);

Supplementary lecture text: Mock 1991 (2), Perrins and Middleton 1985 (1);

Dissection text: Faaborg and Chaplin 1988b (1), instructor's own (8), Pettingill 1990 (5);

Field guide: National Geographic 1983 (3), Peterson 1980, 1984 (11), Pettingill 1990 (3), Robbins et al. field guide 1983 (4).

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Ornithological Literature

Edited by William E. Davis, Jr.

SWALLOW SUMMER. By Charles R. Brown. Univ. Nebraska Press, Lincoln, Nebraska. 1998: xiii + 371 pp., black-and-white photographs. $16.95 (paper).—For the past 15 years, Charles R. Brown and his wife Mary have studied Cliff Swallows (*Petrochelidon pyrrhonota*) at Cedar Point Biological Station in the Sand Hills of western Nebraska. The Browns' research was (and continues to be) highly productive, partly because the swallows proved to be excellent research material. Cliff Swallows make mud nests in colonies that may range from a few birds to thousands. The swallows are relatively easy to capture (but provide the basis for many adventures) and are tolerant of extensive handling. Their natural history is relevant to numerous issues in the basic ecology of birds and to the understanding group behavior of animals.

This book is a non-scientific account of how the Browns came to work on this bird and the trials and tribulations of one season of their studies. Each year they arrive in Nebraska in May in advance of the first swallows. They capture, band, weigh, and measure birds until the swallows stop breeding in late July. With the help of numerous assistants, they have obtained data from thousands of swallows. In fact, their total sample size for some measurements must be in six figures!

The writing is clear, funny, insightful, interesting, and informative. If you have more than a passing interest in swallows, group behavior, or basic avian ecology, you should also read the scientific account, "Coloniality in the Cliff Swallow: the effect of group size on social behavior" (co-authored with Mary Brown; 1996, Univ. Chicago Press), if you have not already done so.

Prairie thunderstorms, clouds of birds, the mysteries of bird behavior, quotes from western movies (especially from "Lonesome Dove"!), the deep pleasures of spending the summer at a field station, the behavior of field assistants, the dirt/frustration/exhaustion of long days in the field, the satisfaction of discovery—these are just a few of the rich threads in the texture of Brown's account. If you have worked for a long time on one species, spent a summer with students at a field station, love western Nebraska, have struggled to fund and run a field research project, or simply would enjoy a good account of how field ornithologists see the world, you will appreciate this book.—CHARLES R. BLEM.

ATLAS OF BREEDING BIRDS OF INDIANA. By John S. Castrale, Edward M. Hopkins, and Charles E. Keller. Available from: Indiana Department of Natural Resources, Customer Service Center, 402 W. Washington St., Rm. W160, Indianapolis, IN 46204. 1998: 388 pp., 14 numbered text figs., 7 tables, 158 range maps. $20 plus $3.50 s&h, $1 sales tax for Indiana residents (cloth).—The Indiana Nongame and Endangered Wildlife Program of the Indiana Department of Natural Resources sponsored this atlas project, coordinating the nearly 600 volunteers and paid "block busters" during the fieldwork conducted from 1985–1990. Workers targeted 647 "priority blocks," west-central of the six blocks of each U.S. Geological Survey 7½′ topographic map of the state. A series of maps depict counties, public lands, rivers, urban areas, natural regions, forested areas (with separate maps for evergreen-deciduous and shrubland-early successional woodlands), agricultural row-crops, pastureland, and marshes and open water. In an attempt to provide some indices of abundance, atlas accounts used Breeding Bird Survey (BBS) and Summer Bird Count (SBC) data for the 1985–1990 period. The SBC uses the county as the sampling area, and counts are conducted on multiple days during June. A table lists in rank order the percentage of blocks in which a species was detected (e.g., American Robin, *Turdus migratorius*, 100%, rank = 1), abundance values and rank for BBS routes, and birds/party hour and rank for SBCs.

A biogeographic analysis by J. Dan Web-

ster includes a table that lists species extinct or extirpated by 1929, species extirpated between 1929 and 1979, possible or sporadic nesters, Twentieth Century additions as breeders, and confirmed breeding species since 1990. The analysis of bird distributions does not correspond well with physiographic patterns, vegetation, distribution of other groups of organisms, or "natural regions." The author suggests birds are poor indicators of biogeography in a small, flat state like Indiana. Major changes this century that have had a major impact on nesting species include the virtual disappearance of the prairies, the drainage and pollution of wetlands, and the fragmentation of forests. The extirpation of prairie, wetlands, and forest interior species, together with a uniform intrusion of alien species has resulted in a more uniform avifauna in the state.

The bulk of the book is devoted to species accounts. Full species accounts accompany the 158 species that were confirmed breeders, supplemented by shorter accounts for 46 species not confirmed as breeders during the atlasing period (including extirpated breeders and those confirmed as breeding since 1990). Each map occupies a full page, with the species account on the facing page. The large size of the maps makes them very easy to read. The species accounts give very brief natural histories synopses, and the bulk of the accounts are concerned with historical distribution comparisons, analysis of the atlas results, and comparisons with bird distributions in the surrounding states of Ohio, Michigan, Illinois, and Kentucky. Each species account is accompanied by a table summarizing the atlas, BBS, and SBC data for north, central, and southern regions of Indiana, as well as statewide.

This is a well-done atlas that is a bargain at $20—the more than 350 references, many to local publications, alone are worth that. It should be of interest to those concerned with bird distribution.—WILLIAM E. DAVIS, JR.

A GUIDE TO THE NESTS, EGGS, AND NESTLINGS OF NORTH AMERICAN BIRDS, SECOND EDITION. By Paul J. Baicich and Colin J. O. Harrison. Academic Press. 1997: 347 pp., 64 color plates, and 103 black and white figures. $22.95 (paper).—This is an updated version of the 1978 edition, and this new edition is a must for the library of anyone interested in the nesting period of North American birds. The guide begins with an introduction that describes a variety of aspects of breeding biology including how and where nests are built; egg shape, color, and size; and clutch size, incubation, hatching, and the nestling period. Keys to nests, eggs, and nestlings are also provided in the introductory pages. The introductory section is followed by a series of individual species accounts. Each species account includes breeding habitat; location, description, size, and materials of the nests; number, shape, size, and color of eggs; breeding season; length of incubation; description of nestlings; length and description of nestling period; and roles of both sexes in these activities.

For many users, the most valuable aspect of this book is the color plates that provide photographs of the eggs of 597 species of North American breeders as well as 147 color drawings of nestlings. While most species' eggs are represented by a single photograph, several with particularly variable eggs are represented by multiple photographs; for example, the authors provide six different photographs of Sandwich Tern (*Sterna sandvicensis*) eggs. Additional information about variation within a species is described in plate legends as well as individual species accounts. Black-and-white drawings are scattered throughout the text to illustrate additional nestlings and a variety of nests.

The second edition of this guide includes substantial information, photographs, and drawings from the first edition; however, it also includes updates and new information that was not in the first edition. Species names (both common and scientific) and taxonomic affinities have been updated to reflect changes since the first edition. Numerous species accounts have been augmented with information about breeding biology, numbers of eggs, and incubation that was missing or not known in the first edition. Species accounts have been added for a number of species that were split from existing species (e.g., Bicknell's Thrush, *Catharus bicknelli*; California Gnatcatcher, *Polioptila californica*; and Island Scrub-Jay, *Aphelocoma insularis*) or have begun to breed

regularly in North America (e.g., Lesser Black-backed Gull, *Larus fuscus*; Buff-collared Nightjar, *Caprimulgus ridgwayi*; and Shiny Cowbird, *Molothrus bonariensis*). The plates have been updated to provide pictures of the eggs of the new species covered in the text and to reflect changes in taxonomic order, species names, and family groups. Another useful change in the revised edition is the grouping of all the plates together in the center of the guide rather than having the plates of nestlings scattered throughout the text pages. This change in format makes the guide easier to use than the first edition. The guide also now includes a selected bibliography of important works used in the revision and information on how to contact the author to obtain specific references for each of the accounts.

Professional and amateur ornithologists will find that this guide provides extensive information about nests and eggs in an easy-to-use format. I would highly recommend *The Guide to Nests, Eggs, and Nestlings of North American Birds* to anyone interested in identifying birds' nests and eggs or learning more about the nest and nestling stage of North American birds.—SARA R. MORRIS.

BREEDING BIRDS OF WASHINGTON STATE: LOCATION DATA AND PREDICTED DISTRIBUTIONS. By Michael R. Smith, Philip W. Mattocks, Jr., and Kelly M. Cassidy. Available from Seattle Audubon Society, 8050–35th Avenue NE, Seattle, WA 98115. 1997: 538 pp., 10 numbered text figs., 6 tables, 244 range maps. $30 plus $3 s&h (paper).—The authors attempt to fill two roles with this book: compilation of the Seattle Audubon Society's breeding bird atlas project, and a part of the final report of the Washington State Gap Analysis project (administered by the National Biological Service). The goals of this aspect of the Gap Project were to map existing land cover, and model the breeding distributions of birds. The book is divided into an introductory chapter (22 pp.) and 258 species accounts that include 244 maps (489 pp.).

The introductory chapter traces the history of the Atlas project and summarizes the data collected and analyzed. Over 600 volunteers contributed data over the decade beginning in 1985. The sampling unit was a block of nine square miles that constituted one quarter of a township, for a total of 7912 blocks. Data provided by the Washington Department of Fish and Wildlife, particularly from their shrub-steppe bird study and National Heritage database, were included. Coverage of blocks was incomplete, with 56% containing at least one "possible" species record, 51% a "probable" record, and 44% a "confirmed" record. More than 10 species were confirmed breeders in 6% of the blocks (the highest number of confirmed species in a block was 67). The authors discuss the biases in the data, including the concentration of records from more developed areas of the state. They also point out that records do not reflect abundance, and give the delightful example: "a confirmed breeding record of a Ruby-crowned Kinglet in the Ponderosa Pine zone in the Blue Mountains (where the species is uncommon, but can usually be found) occupies the same area on the map as a confirmed record derived from the Subalpine Fir zone, where Ruby-crowned Kinglets are best measured by the ton."

For most species models predicting breeding distribution (extent of a species' breeding habitat) were prepared and appeared on the species' distribution map as "Habitats in core zones" with, in some cases, an additional "Habitats in peripheral zones" presented in a lighter shade of gray. Habitats were selected from a satellite image landcover map of the state. Bird-habitat associations were developed from literature reviews, location of breeding records, and consultation with experts. The introductory chapter detailed the modeling process and mapping processes, albeit with a touch of jargonese (e.g., "Each scene was spectrally clustered into 120 to 256 spectral classes using bands 1, 2, 3, 4, 5, and 7" or "the presumption that error in a cover is equal to the product of the errors in each layer comprising that cover is an over-simplification. The effect of an error in a source layer upon a derived cover depends on what is being derived."). Ecoregions, vegetation, and vegetation zones are detailed in tables, a black-and-white map, and in two color plates.

Each species account is divided into three parts, the first "Breeding Status and Distribution," the second "Model" gives the char-

acteristics of the model predicting the breeding distribution, and the third "comments," provides aspects of the species' biology. The latter contains such information as maximum abundance numbers for island nesting species, comments on taxonomy, e.g., American (*Corvus brachyrhynochos*) and Northwestern (*C. caurinus*) crows, and an historical perspective on the species. I found the "comments" sections particularly informative.

This is an interesting book. It is a hybrid volume, and thus provides a great deal of information on habitat and computer modeling not usually found in breeding bird atlases, but is also somewhat jarring because of the contrast of sophisticated jargon associated with the Gap Analysis and the more usual distribution descriptions associated with atlas projects. The atlas coverage seems sparse and I wonder why Breeding Bird Survey data weren't used to provide a better measure of bird abundance. As is usually the case, the more than 200 references, many from local journals and unpublished sources, are a gold mine of regional information. Certainly this book should be part of the library of every serious student of bird distribution, and all academic libraries.—WILLIAM E. DAVIS, JR.

MADE FOR EACH OTHER: A SYMBIOSIS OF BIRDS AND PINES. By Ronald M. Lanner, Oxford Univ. Press, New York, New York. 1996: 160 pp., 14 chapters, 24 figures, 8 tables, and 15 color photographs on 4 plates. $35.00 (cloth).—This slim book interweaves a description of symbiosis on a "grand scale" between some corvids and over twenty species of pines across "vast tracts of North American and Asian wildland" with the coevolutionary story of the Clark's Nutcracker (*Nucifraga columbiana*) and whitebark pine (*Pinus albicaulis*) of the western United States. The author makes the case that the nutcracker-pine relationship is a strong mutualism because nutcrackers are the most important dispersal agents of the pine seeds and the pine seeds are a nutrient-rich food essential for nutcracker survival. The critical message, delivered in the final chapter, "Is the Keystone Slipping?," is an alert that serious threats to the whitebark pine may diminish populations of the nutcracker and other animal species that depend on the pine seeds.

This is a book for pine lovers. To support his argument for the mutualism between corvids and pines, Lanner examines the phylogeny, comparative morphology, and ecology of pines, particularly the 35 species of "soft pines" in the subgenus *Strobus*. This group of species has a high proportion of species with wingless seeds: a critical adaptation to dispersal by corvids. The five species of stone pines—Eurasian and one North American—that are close mutualists with the Eurasian (*Nucifraga caryocatactes*) and Clark's nutcrackers receive the most attention. Characteristics of stone pine cone fertilization and development, and seed germination and nutritional content, are described in detail. Some of these descriptions are less relevant to the main thesis of the book than others, but they provide a rich natural history.

A review of the family Corvidae quickly focuses on the "pine birds": the nutcrackers and the Pinyon Jay (*Gymnorhinus cyanocephalus*). "Pine bird" adaptations to a diet of pine seeds are long bills, the ability to carry numbers of pine seeds, and well-developed spatial memory for retrieving cached seeds. The foundation for the pine-corvid mutualism, including experimental evidence that Clark's Nutcrackers use fixed objects as visual cues to find food caches, is provided primarily by the research of Diana Tomback, Stephen Vander Wall, Russell Balda, and Lanner's own work on seed dispersal by birds. Lanner is careful to point out that nutcrackers are not completely dependent on a single species of pine. He notes that nutcrackers use a variety of other pine seeds and foods and migrate (irrupt) when the pine seed crop fails. However, nestlings are fed pine nuts that were cached almost exclusively, and cached foods are used extensively during fall, winter, and spring when other foods are scarce.

In Lanner's view winged pine seeds are ancestral to wingless seeds, and corvids provide the selection pressure to make this transition. He presents a scenario for evolution of wingless seeds in two groups of closely related pine species: the *P. ayachuite-strobifomis-flexilis* complex in Mexico and the western United States and the *P. parviflora* complex in eastern Asia. Pine seeds cached by corvids

are less likely to dessicate and more likely to germinate than seeds dispersed by the wind. Therefore, in drier climates, characteristics in pines that enhance dispersal by corvids—vertical fruiting branches, sessile cones, nonopening "breakaway" scales, seed-retaining cone cores, and large, wingless seeds—would be advantageous.

Lanner's two main theses—whitebark pine depends on Clark's Nutcracker for effective seed dispersal, and the whitebark pine is a keystone species—superficially seem difficult to reconcile. Many animal species (birds, squirrels, and bears) extract, move, and eat whitebark pine seeds (the keystone concept), but the nutcracker is essentially the only agent of seed dispersal (a tight mutualism). The final chapter ("Is the Keystone Slipping?") presents the case that whitebark pine is a species upon which Clark's Nutcracker, red squirrel (*Tamiasciurus hudsonicus*), and grizzly bear (*Ursus arctos*) depend to varying degrees. The whitebark pine is seriously threatened by "competition from more shade-tolerant trees due to fire exclusion; heightened bark beetle attacks, also engendered by fire exclusion; loss of habitat through global warming; and quick death from a parasitic fungus." If these threats severely diminish populations of whitebark pine, over the long term and in a diffuse ways, the nutcracker, and to a lesser extent, the red squirrel and grizzly bear will suffer.

The writing is clear and the pace brisk. Figures and tables are used judiciously and the plates are excellent. Some readers may object to instances of anthropomorphism ("Whitebark pine takes its seeds very seriously indeed when it comes to distributing the tree's resources.") and unabashedly adaptationist interpretations, but this is perhaps expected in a book directed to a general readership. Details of pine phylogeny and the uses of pine nuts by people help to flesh out the story. I heartily recommend this book to all interested in good natural history writing and forest ecology in particular.—R. TODD ENGSTROM.

SKUAS AND JAEGERS: A GUIDE TO THE SKUAS AND JAEGERS OF THE WORLD. Klaus Malling Olsen and Hans Larsson. Yale University Press, New Haven and London. 1997: 190 p. 12 color and 1 black-and-white plate, 156 photographs, 20 of these in color and 7 maps. $35.00 (cloth).—This is an excellent field guide to the skuas and jaegers, and the only current reference I know that correctly illustrates and describes the juvenal and winter plumages of all seven species. For this reason, the book is an essential reference for all interested in seabird identification. The basic, alternate, and juvenal plumages of three jaeger and four skua species are all illustrated with attractive color paintings by Larsson; most or all of these are depicted in clear photographs as well. A painting of adults of the four species of skuas is oddly reproduced in black-and-white; presumably this was done to save costs—it slightly mars the otherwise excellent graphic presentation.

The book is organized into an Introductory section of 28 pages that includes such topics as "Breeding Behavior", "Skuas and Man", and "Observing Skuas in the Field"; followed by the species accounts which form the main body of the text. The species accounts contain sections on identification, geographical variation, food, and range during migration and winter (including maps). Compared to the obvious precision and attention to detail characteristic of the species accounts, I found the Introductory sections to be somewhat cursory and containing a number of questionable statements. For example, on page 9 it is stated that "Unlike gulls, skuas have supraorbital salt glands . . . ."—gulls certainly have these as well, as anyone who has watched "runny-nosed" gulls at the seashore probably knows. The dogma about clockwise migrations around the North Pacific and North Atlantic Oceans by South Polar Skuas is perpetuated, despite the lack of evidence to support the notion that any individual bird follows such a path. My final quibble is about a point of long-standing confusion about the occurrence of Brown Skuas (*Catharacta skua*) in the Caribbean. While the confusion is obviously no fault of the authors, this book would have been an ideal forum for the settling of this issue. I leave it to the reader to puzzle out whether the recovered banded skuas from "Guadeloupe" and the "Lesser Antilles" are one or two individuals, and how likely it is that either were misidentified South Polar

Skuas (*C. maccormicki*). Recent sightings from the North Atlantic suggest that Brown Skuas may be transequatorial migrants.

To me, the most novel and interesting information in this book pertains to recent observations of migrating skuas and jaegers, both from land and from ships at sea. Not only have some remarkable numbers of these birds been observed, but compilations of such observations suggest they could be used as estimates of reproductive success the previous season. This is due to correspondence within years of the proportions of juvenile birds seen. In all, the authors are to be congratulated. This is a valuable and long overdue work, skillfully and artfully executed.—RICHARD R. VEIT.

JOHN ABBOT'S BIRDS OF GEORGIA: SELECTED DRAWINGS FROM THE HOUGHTON LIBRARY, HARVARD UNIVERSITY. Introduction and commentary by Vivian Rogers-Price. Beehive Press, Savannah, Georgia. 1997: vii-xlii, 25 color plates and facing-page commentary, unnumbered and unpaginated. $125 (cloth with linen slipcase).—This publication presents the first color reproductions, in book form, of bird paintings of John Abbot (1751–1840), an English-born artist-naturalist who spent most of his long adult life in Georgia. He completed more than 5000 watercolors of natural history subjects including more than a thousand of birds, most of which are extant, and another thousand of insects, their life cycles and food plants. The remainder includes everything from mites and ticks to crabs and millipedes. Abbot's father had encouraged his early natural history illustration predilection, providing him with an abundance of fine bird books and professional instruction from teacher Jacob Bonneau. At age 22 Abbot sailed to America and landed in Virginia where he remained until the rumblings preceding the American Revolution prodded him into moving to the then less militant Georgia. He remained there for the rest of his life where he supported himself largely through the sale of natural history collections and watercolor paintings that were eagerly sought by Europeans from his agent in London, John Francillon. Abbot published little himself, but in England several volumes about butterflies, moths, and other insects were illustrated by his work. John Latham used Abbot's drawings and specimens in his book *General History of Birds* (1821–1824). Abbot met and aided Alexander Wilson in the compilation of his *American Ornithology,* and aided George Ord in the completion of this major work following Wilson's untimely death.

Probably at least partially because his work was published by others and because of his own parochialism, John Abbot's bird work was largely eclipsed by Wilson and Audubon. However, Abbot's style of presentation was apparently modeled after George Edwards, and similar to William Bartram's, with stylized foregrounds and birds perched on dwarfed trees. Abbot did not progress artistically beyond the limitation of this approach, which Wilson and Audubon did, and by the time of his death in 1840, his bird portraits appear rather archaic. Nevertheless, I find it remarkable that nearly two centuries elapsed before a selection of this important American bird artist's watercolor paintings of birds were published.

This large-format (27 × 31 cm) book begins with a 17-page introduction that provides a biographical sketch of Abbot's life, highlighting his natural history collections and paintings and his European colleagues and patrons. It is a scholarly work, with 115 endnotes that, in small type-face, at 19 pages much exceed the length of the introduction. The heart of the book is the 25 watercolors of birds that are reproduced at the same size as the originals. Each of the paintings is accompanied on a facing page by a brief commentary and any of Abbot's notes that relate to the species. The book concludes with the history and final disposition of 12 collections of Abbot's original paintings, including the collection of 181 bird portraits, painted from 1801–1810, from which the paintings reproduced in this book were selected.

I compared the plates with the originals at the Houghton Library at Harvard University. The quality of reproduction was variable but generally good (the American Oystercatcher, *Haematopus palliatus,* was faded in appearance but the Mourning Dove, *Zenaida macroura,* was as crisp as the original). The backgrounds in the reproductions were darker

and buffier than the originals and made the reproductions warmer than the originals, but muted the colors, especially the greens somewhat; and the contrast was not as crisp. This was particularly a problem for the light-colored egret and heron paintings. The selection of paintings includes a hummingbird, which was the only bird Abbot ever painted in flight, a signed and dated Bald Eagle (*Haliaeetus leucocephalus*), a vulture, an owl, three woodpeckers, one sparrow, one wren, a nighthawk, a dove, a crane, seven herons and ibises, an oystercatcher, a tern, and four ducks. I found the heavy emphasis on herons, ibises, and ducks somewhat perplexing, although many, like the preening Wood Duck (*Aix sponsa*), illustrated interesting poses or behaviors.

I have a strong bias against footnotes and endnotes, and found flipping back and forth from the introductory text to the endnotes annoying. The commentary facing each plate could have been expanded—there is a lot of empty space. Minor problems aside, this is an important work—thoroughly researched and attractively presented. I commend the Beehive Foundation for making Abott's important work accessible. I recommend the book to those with particular interest in the history of ornithology or bird art. The price may limit sales, but every academic library should have a copy.—WILLIAM E. DAVIS, JR.

OISEAUX DE LA RÉUNION. By Nicolas Barré, Armand Barau, and Christian Jouanin, illustrated by Nicolas Barré. Second edition, revised and corrected by Nicolas Barré and Christian Jouanin. Les Éditions du Pacifique, 62 rue du Couédic, 75014 Paris. 1996: 207 pp., 10 color plates, numerous color and black-and-white text illustrations, bibliography, indexes. ISBN 2-87868-027-8. Cloth. No price given.—Although only ten pages longer, the second edition of "Oiseaux de la Réunion" is an improved and slightly larger-sized volume (21 × 15 instead of 20 × 12.5 cm) than the first (which I reviewed in 1983, Auk 100:541–543). The disadvantage of a slightly larger size, of course, is that the new book fits less easily in a pocket than the original edition did. As the first edition had been out of print since 1990, the need for a second edition had been felt for quite some time. The problem was that the two original authors were no longer available for this job. Sadly, one of them, Armand Barau, who was an agronomist, had died in 1987, and the second author and illustrator, Nicolas Barré, a veterinarian, had left Réunion in 1982, the year the first edition was published. In the preface to the second edition, Christian Jouanin, Associate at the Muséum national d'histoire naturelle in Paris, who brought the project of a second edition to fruition, explains how Armand Barau's widow and Nicolas Barré persuaded him to undertake the revision. We are fortunate that he accepted this task. This important guide (which, when still in print, was difficult to get, as one had to write the authors in Réunion in order to obtain copies) has now been handsomely produced by the Éditions du Pacifique in Paris.

Although the text of the second edition is quite similar to that of the first, Jouanin has brought the species accounts up to date and has incorporated much new information, both published and unpublished, that has been gathered on the status and distribution of the birds of Réunion by a number of workers since the early 1980s. Eight of the ten color plates in the second edition are the same as the eight of the first, except for their numbering: Plates VI, VIII, and X were numbered as V, VII, and VIII, respectively, in the first edition. Two plates are new: numbers VII (including seven species of kites, frigate-birds, plovers, terns, and ducks; pages 148–149) and IX (including 4 morphs of the endemic white-eye *Zosterops borbonicus borbonicus* and several plumage variations in the endemic chat *Saxicola tectes*; pages 178–179; a very welcome addition). Interestingly, the eight original plates are better reproduced in the second than in the first edition (at least in my copies). They are fresher, their colors are crisper, and their slightly larger size mean that the birds on each plate are slightly larger, an improvement in my opinion. As in the first edition, the second has numerous black-and-white text illustrations. Not all original drawings are included, however, and some have been redrawn. For example, the attractive and evocative drawings of several species of seabirds and a fishing boat (first edition, page 89) and of shorebirds on a mudflat (first edition,

page 131) have been omitted from the second edition, a pity. The attitudes of plovers, fresh from a field sketchbook on page 138 of the first edition, has been redrawn for the second edition (page 132), but is now stiff and artistically much less interesting. A novel feature is the inclusion of a color portrait of each species, taken from the plates, next to the name of each species in the species accounts. As in the first edition, the introductory sections are illustrated with color photographs of habitats of Réunion. Whereas there were 6 such photographs in the first edition, the second has 12, thus giving the potential visitor a better overview of these landscapes.

In addition to the species accounts and the plates, this volume includes an excellent description of Réunion (pages 14–23); a thorough and fascinating (if sad) review of the past avifauna (pages 26–52, illustrated with nicely reproduced color plates of extinct species, borrowed from older publications); a detailed presentation of the modern avifauna (pages 53–76, including hints about bird watching and information about conservation); and suggestions about how to use the guide. The book ends with a bibliography (pages 194–199) and four indices (French, Latin, English, and Créole names). One regret: this book does not have a map showing the position of Réunion in the Indian Ocean (this was true of the first edition also).

Beautifully produced, full of carefully researched information, easy to use thanks to its user-friendly typography; I strongly recommend this book to all students of insular avifaunas. No one visiting Réunion can be without it. As I wrote in my review of the first edition, this book "should be mandatory reading for all school children of Réunion taking courses on the geography of their magnificent island." My thanks go to Christian Jouanin for having seen this second edition through the press.—FRANÇOIS VUILLEUMIER.

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ANTILLEAN SHORT-EARED OWLS INVADE SOUTHERN FLORIDA

WAYNE HOFFMAN,[1] GLEN E. WOOLFENDEN,[2] AND P. WILLIAM SMITH[3]

ABSTRACT.—Recently, Short-eared Owls (*Asio flammeus*) have invaded extreme southern Florida during spring and summer, most appear to be post-fledging dispersers. Morphological and plumage characteristics identify the specimens as coming from the Antilles, most likely from Cuba, where numbers and range have expanded greatly in recent years. This dispersal continues a trend that began in other bird species more than half a century ago. Since 1932 about one landbird species per decade has colonized southern Florida from the Antilles. *Received 27 May 1998, accepted 30 Nov. 1998.*

During the last two decades, Short-eared Owls (*Asio flammeus*) have occurred with increasing frequency in extreme southern Florida, especially from March through September. In the absence of specimens, these reports were assumed to represent individuals of the nominate race *A. flammeus flammeus,* which was the only form of this polytypic species known from the North American continent. *Asio f. flammeus* is Holarctic; in the western hemisphere it breeds in northern North America and migrates south as far as southern United States, Mexico, and rarely the West Indies (American Ornithologists' Union 1957, 1998). During the 1990s we obtained several specimens of Short-eared Owls from extreme southern Florida. Here we summarize all recent records and reports of Short-eared Owls from southern Florida, describe the characteristics of Holarctic and Antillean Short-eared Owls and conclude that most of the recent spring–summer records are from an Antillean population, and briefly review their nomenclature. Finally, we discuss possible causes for the dispersal of these owls into Florida and their potential for colonizing the North American continent.

SPECIMENS, PHOTOGRAPHS AND REPORTS

Specimens.—Between July 1990 and March 1998, we obtained eight dead Short-eared Owls from the Florida Keys, Monroe County, Florida. Three of the six males showed no molt, while three showed light, scattered body molt. All six males had small testes and all had extensive black feathering around the eyes, which in the nominate race typifies juvenal plumage (Holt and Leisure 1993). One female (GEW 5902, 25 May 1996, ovary 15 × 4 mm, largest ovum 1 mm, substantial body molt) also appeared to be juvenile, but the other (GEW 5889, late April 1994, ovary 17 ×

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←

FRONTISPIECE. Antillean Short-eared Owl photographed in Ft. Zachary Taylor State Park, Key West, Monroe County, Florida on 4 April 1994 by Wayne Hoffman.

4, largest ovum 2 mm) had worn plumage and possibly a regressing brood patch, and might have been an adult.

Comparative material included five Short-eared Owl specimens from the Antilles, four from the southern Florida mainland, and 46 from elsewhere in North America. In June 1995 Orlando Garrido kindly loaned us an unsexed adult specimen (MNHN-1595) collected in Sancti Spiritus Province, Cuba. In 1996 Garrido donated to the Archbold Biological Station collections a male specimen collected near Havana (GEW 5925). We also examined two nestlings collected in the Dominican Republic in November 1963 (LSUMZ 142354 and 142355; Schwartz and Klinikowski 1965). The four mainland specimens, all from Dade County, were two from Everglades National Park (EVER 5035, collected 5 January 1971; GEW 5890, collected 9 December 1990) and two in the University of Miami Research Collections (UMRC 948, collected 7 February 1956; UMRC 5387, collected 8 November 1966), which now are in the collections at Archbold Biological Station.

In April 1997, Hoffman measured six specimens of the Holarctic *Asio flammeus flammeus* in the Pennsylvania State University collections and 40 specimens in the Carnegie Museum collections. All were taken in North America throughout the year. The few specimens with missing or incompletely grown primaries or central rectrices were excluded from analysis. Hoffman also examined and measured the single Puerto Rican specimen in the Carnegie Museum.

Measurements taken include lengths of wing (flattened), tail, tarsus, and culmen from the cere. Measurements were taken as described by Palmer (1962) and Cramp and coworkers (1977). Tarsi are difficult to measure on the feathered feet of owls, so a dissecting probe was used to assist in locating the measuring points on the posterior of the intertarsal joint and the anterior of the middle toe articulation with the tarsometatarsus.

Photographs and reports.—We examined photographs of six individuals that did not become specimens: three from the Dry Tortugas, two from other of the Florida Keys, and one from the Gulf of Mexico off Hernando County. We reviewed reports of Short-eared Owls from Florida published in *Audubon Field Notes* and *American Birds* (Loftin et al. 1991) and evaluated other written and verbal reports of these owls in southern Florida since 1978.

RESULTS

Current status of Short-eared Owls in southern Florida.—Our review of citations in *Audubon Field Notes* and *American Birds* yielded about 68 reports of Short-eared Owls in Florida before 1978. With one exception, a bird seen 14 June 1963 at Lakeport, Glades County, all pre-1978 reports were of occurrences between early October and late March. We obtained information on 30 occurrences of 33–37 Short-eared Owls in Florida since 1978, including 16 records (specimens and photographs) and 14 reports (no tangible evidence). Twenty-three of the 30 appeared in spring and summer, outside the early October–late March dates dominating the earlier period. During spring–summer 1994 the influx seemed particularly heavy. The first bird was located at Ft. Taylor State Recreation Area in Key West, 25 March (photographed on 4 April). It was joined by a second bird in mid-April; both disappeared by mid-May. Meanwhile a birding tour located three birds at the Dry Tortugas on 8 April (Woolfenden, pers. obs.). One was picked up there in weakened condition on 18 April and died while in transit to Key West for treatment (GEW 5889). On 8 June, W. B. Robertson, Jr. flushed a group of four owls on Long Key, Dry Tortugas. Thus, a minimum of five, possibly as many as nine, owls were found in southern Florida in spring 1994. Another record that summer was of an individual plucked from the water offshore of Hernando Co., in June (Table 1). The dates of occurrence of these records and reports suggest a source other than the Holarctic. The specimens we have obtained allowed us to test this hypothesis using geographic variation described for Short-eared Owls.

Structural and plumage differences between the Antillean and Holarctic Short-eared Owls.—Based on Ridgway (1914) and Wetmore (1928), and the specimens we examined, Antillean Short-eared Owls differ from Holarctic Short-eared Owls in size, proportions, and plumage. These differences appear adequate to distinguish all specimens in the hand, and to allow identification of birds observed closely in the field. They also appear sufficient

TABLE 1. Short-eared Owl records and reports from southern Florida since 1978.

Year	Dates	Location	Source	Documentation	Origin
1978	21–22 Jun.	Dry Tortugas	Hoffman et al. 1979	Photographs	Antilles
1979	24 Nov.	Virginia Key	Am. Birds 34:154	—	—
1984	Winter 1983–84	Flamingo	P. and M. Brown, pers. comm.	—	—
1984	11–12 Apr.	Dry Tortugas	Am. Birds 38:901	—	—
1984	30 Dec.	ENP main road	Am. Birds 39:160	—	—
1985	27–29 Apr.	Dry Tortugas	Am. Birds 39:290	Published photograph	Antilles
1986	19–21 Apr.	Dry Tortugas (2 birds)	Am. Birds 40:461	—	—
1987	late Mar.–25 May	Dry Tortugas	Am. Birds 41:421	—	—
1987	24 Aug.	Bottle Key, Florida Bay	R. Bowman, P. Cavanagh, pers. comm.	Photographs	Antilles
1988	Aug.	Big Pine Key		Specimen, lost	Antilles?
1989	26 Apr.	Big Pine Key	W. B. Robertson, Jr., pers. comm.	Wing & leg saved, ENP	Antilles
1989	5 May	Dry Tortugas	Am. Birds 43:469	—	—
1990	28 Jul.	Dry Tortugas	M. Eng, pers. comm.	Specimen, ABS, GEW 5861	Antilles
1990	10 Dec.	ENP main road		Specimen, ABS, GEW 5890	Holarctic
1992	10 Apr.	Key West		Specimen, ABS, GEW 5862	Antilles
1993	18 Apr.	Marathon		Specimen, ABS, GEW 5886	Antilles
1993	10 Jun.	Dry Tortugas (2 birds)	W. B. Robertson, Jr., pers. comm.	—	—
1994	25 Mar.–early May	Key West (2 birds)	F. & J. Cheeseman, pers. comm.	Photographs	Antilles
1994	8 Apr.	Dry Tortugas (3 birds)	G. E. Woolfenden	Specimen, ABS, GEW 5889	Antilles
1994	8 Jun.	Dry Tortugas (4 birds)	W. B. Robertson, Jr., pers. comm.	—	—
1994	early Jun.	off Hernando Co.	R. Collins, pers. comm.	Photographs	Antilles
1994	3 Sept.	Sugarloaf Creek	W. Hoffman	—	—
1994	1 Nov.	Dry Tortugas	W. B. Robertson, Jr., pers. comm.	—	—
1995	11 Mar.	Key West		Specimen, ABS, GEW 5892	Antilles
1995	26 Jul.	Grassy Key		Specimen, ABS, GEW 5900	Antilles
1996	25 May	Marathon		Specimen, ABS, GEW 5902	Antilles
1996	17 Jul.	Marathon	S. Culley, pers. comm.	—	Antilles
1997	28 April	Dry Tortugas	D. Friedman, pers. comm.	Photographs, D. Friedman	Antilles
1998	12 March	Key Largo		Specimen, ABS, GEW 5930	Antilles
1998	17 April	Dry Tortugas	W. Hoffman	—	Antilles
	Totals	32–37 birds	—	8 specimens	Antilles
				6 photographic	Antilles
				1 specimen	Holarctic

TABLE 2. Measurements of Short-eared Owl specimens. All measurements (in mm) taken by Hoffman. Statistical comparisons of means are by Student's *t*-test (*t*), unpaired. Probability (*P*) of equal means is two-tailed.

		A. f. flammeus			West Indian				
Measurement	Sex	*n*	Mean	(Range)	*n*	Mean	(Range)	*t*	*P*
Wing	M	25	313.8	(306–323)	8	289.8	(286–291)	13.77	<0.001
Wing	F	24	316.3	(308–325)	3	294.7	(292–299)	8.30	<0.001
Wing	both	49	315.0	(306–325)	11	291.0	(286–299)	16.05	<0.001
Tail	M	25	142.0	(133–148)	8	132.8	(127–141)	5.51	<0.001
Tail	F	24	146.1	(134–153)	3	140.7	(136–146)	1.68	>0.05
Tail	both	49	144.0	(133–153)	11	134.9	(127–146)	5.25	<0.001
Tarsus	M	25	42.7	(38–46)	8	52.2	(50–53.5)	10.28	<0.001
Tarsus	F	24	43.7	(39–46)	3	50.7	(50–54)	5.55	<0.001
Tarsus	both	49	43.2	(38–46)	11	51.8	(50–54)	11.67	<0.000
Culmen	M	24	26.3	(24.0–28.0)	8	28.9	(27.8–29.6)	5.21	<0.001
Culmen	F	24	26.2	(24.0–28.3)	3	29.8	(29.5–30.1)	4.51	<0.013
Culmen	both	48	26.3	(24.0–28.3)	11	29.1	(27.8–30.1)	6.94	<0.001

to distinguish Antillean specimens from all other members of *Asio flammeus*.

Compared to Holarctic *Asio f. flammeus*, Antillean Short-eared Owls have shorter wings and tails, longer tarsi, and slightly larger bills (Table 2). Male and female *A. f. flammeus* overlapped broadly for all measurements, and the Antillean male and female specimens overlapped broadly in tail and tarsus measurements. No overlap existed between *A. f. flammeus* and the Antillean specimens in length of the wing, tarsus, and culmen. The two populations overlapped substantially only in tail length. Because of the broad overlap between the sexes for most measurements, tests of significant mensural differences between the groups were run for both sexes combined as well as for males and females separately. Differences between the groups were highly significant for all comparisons except tail length among females (Table 2). Hoffman's measurements of *A. f. flammeus* specimens are similar to those published in Cramp and coworkers (1985), except that the culmen measurements averaged 3 mm shorter, suggesting a methodological difference. Ridgway (1914), Wetmore (1928), and Garrido (1984) have published wing measurements for Antillean owls, and Marshall (pers. comm.) provided measurements on six specimens at the US National Museum (Table 3). Together, these sources provided measurements of 15 specimens (five males, three females, seven unsexed); wing lengths ranged from 274 to 300 mm, which are similar to ours (286–299 mm).

The most notable plumage differences involve coloration of the upper back and the underparts (Fig. 1). On Holarctic birds the contour feathers of the upper back, between and anterior to the scapulars, are mostly tawny with a dark brown central stripe. On Antillean birds these back feathers are mostly dark brown with tawny edgings. As a result the upper back of Holarctic birds appears distinctly striped, whereas the backs of Antillean birds appear overall dark brown, or dark brown with obscure tawny mottling. The underparts of *A. f. flammeus* are heavily streaked with dark brown on a pale tawny to whitish background (Fig. 1). Streaks are broadest and most dense on the upper breast, and gradually become narrower and more sparse posteriorly. The streaked feathers most posterior are located on or near the knee joints. The underparts of the Antillean owls are much more buffy overall. The streaking is similar on the upper breast, but abruptly becomes much narrower and more sparse at mid-breast. The lower breast and belly are mostly unstreaked with a few narrow streaks (less than 2 mm wide) on the flanks. The feathering on and around the knee joints is unstreaked. The difference in pattern and coloration of the underparts was noted as early as 1770 (Buffon *in* Wetmore and Swales 1931). Other plumage differences include the color of the upper tail coverts (fairly dark brown in Antillean birds versus

TABLE 3. Measurements (in mm) of Short-eared Owls, from the literature.

Sex	Taxon	*n*	Wing[a]	Tail[a]	Tarsus[a]	Culmen[a]	Source
Male	*flammeus*	varies[b]	315 (304–326)	142 (134–152)	44.5 (42.8–46.0)	28.5 (27.5–29.4)	Cramp and coworkers 1985
	domingensis	1	294				Wetmore 1928
	portoricencis	2	283 (280–285)				NMNH 573526, 354499
	Cuban	2	280, 285				NHMH (on loan)
Female	*flammeus*	varies[c]	319 (309–331)	144 (137–154)	46.2 (44.5–48.1)	29.0 (27.7–29.8)	Cramp and coworkers 1985
	domingensis	1	298				Wetmore 1928
	portoricensis	2	285				NMNH 358579, 307978
Unsexed	Cuban	varies[d]	292 (285–300)	140		?[e]	Garrido 1984
	portoricensis	4	277 (274–281)				Wetmore 1928
	portoricensis	varies[f]	278 (274–286)	131 (126–136)		?[e]	Ridgway 1914

[a] Mean (range).
[b] n = 39 for wing and tail; n = 16 for tarsus and culmen.
[c] n = 28 for wing; n = 32 for tail; n = 14 for tarsus; n = 12 for culmen.
[d] n = 3 for wing; n = 1 for tail.
[e] Ridgway (1914) and Garrido (1984) measured culmen only to the cere. Ridgway reported mean = 17.3 mm (n = 3) and Garrido 17.3 mm (n = 1). In comparison, Cramp and coworkers (1985) reported means to cere of 16.7 mm (16 males) and 16.9 mm (12 females) for *A. f. flammeus*.
[f] n = 3 for wing; n = 4 for tail.

tawny yellow in *A. f. flammeus*). The sides of the head just behind the lateral edges of the facial disk have an unmarked brown patch not found in *A. f. flammeus*. The dark bars on the rectrices also tend to be more complete and have straighter margins in the Antillean birds.

The feathering of the feet also differs between Holarctic and Antillean birds. In *Asio f. flammeus* the tarsi and the upper surfaces and sides of the toes are densely covered by fine tawny feathers. On Antillean birds, the feathering of the toes is restricted to the dorsal surfaces and terminates 3–6 mm from the talons. The featherless skin of the under surfaces extends up the sides of the toes to near their tops. Feathering on the toes is also more sparse, with exposed skin showing between individual feathers on museum specimens. The feathers on the tarsi and toes are shorter in the Antillean birds (ca 6 mm versus 16 mm on the posterior surface midway along the tarsus and ca 3 mm versus 6 mm long on the proximal phalanx of the middle toe).

Photographs of the Antillean owls appear to show more prominent "ear" tufts than do *A. f. flammeus,* but an attempt to measure the tufts on the specimens at ABS failed to show differences (tuft length 19–29 mm for 10 Antillean owls; 20–27 mm for 3 *flammeus*). The surrounding head feathers appeared shorter on the Antillean birds so the tufts may in fact protrude farther, and possibly the Antillean owls are more likely to erect the tufts when confronted by photographers.

The Antillean birds appear to weigh substantially less than northern birds. Three seemingly non-emaciated males of our Florida specimens weighed 260 g, 280 g, and 299 g, and the two non-emaciated females 274 g and 288 g. In comparison, mean weights of *A. f. flammeus* are 315 g for males, and 378 g and 411 g for two samples of females (Holt and Leasure 1993).

Comparison of southern Florida specimens with a series from the Greater Antilles.—We sent the first two specimens we obtained (GEW 5861 and GEW 5862) to Joe T. Marshall at the National Museum of Natural History (NMNH) who compared them with a series of eight specimens from the Greater Antilles (six from Puerto Rico and two from Cuba). He informed us (pers. comm.) that the Florida specimens were similar to these An-

FIG. 1. Specimens of *Asio f. domingensis* and *Asio f. flammeus*. A. Dorsal view. Left row from top: *Asio. f. domingensis*; 1 unsexed adult from Cuba, 1 female from Florida, and 4 males from Florida. Right row from top: *Asio. f. flammeus*; 3 females from mainland southern Florida, 1 female from Grand Turk. B. Ventral view. Left row from top: *Asio. f. domingensis*; 1 unsexed adult from Cuba, 1 female from Florida, and 4 males from Florida. Right row from top: *Asio. f. flammeus*; 3 females from mainland southern Florida, 1 female from Grand Turk. Photograph by Reed Bowman.

tillean birds in wing length and back color and pattern, but had paler underparts and smaller bills. He did not assign them unequivocally to any named population.

Comparison of southern Florida specimens with Cuban specimens.—Five of the eight Florida owls not referable to *A. f. flammeus* were compared with the unsexed Cuban specimen (MNHN 1595), and all eight were compared to the second Cuban specimen (GEW 5925). The first four males from Florida had somewhat paler underparts than the first Cuban specimen (MNHN 1595), but the Florida female (GEW 5889) had slightly darker underparts. As is true for *A. f. flammeus* (Holt and Leasure 1993), females of the Antillean form may have darker underparts than males. The second Cuban specimen (GEW 5925) has some darker markings dorsally than most of the Florida specimens but otherwise appeared similar. The Florida specimens also agreed in detail with the Cuban specimens in the foot-feathering characteristics. We conclude that these eight specimens from southern Florida are vagrants from the Greater Antilles, and probably originate from Cuba. We suspect the slightly paler underparts and smaller bill size noted by Marshall are characteristics of age or sex.

Analysis of photographs.—The photographs of six owls from Florida agree in plumage with the eight specimens described above, so we consider them Antillean (Table 1). The first of these was discovered by Hoffman on Bush Key, Dry Tortugas, on 21 June 1978 and photographed in the hand by Barbara Kittleson (Hoffman et al. 1979). When the 1990 specimen was recognized as resembling Antillean representatives of the *Asio flammeus* species-group, we re-examined the photographs and found them to show the dark back and finely streaked buffy underparts of Antillean birds. The second owl was photographed by Howard P. Langridge in April 1985 (Kale 1985). It shows extensive black surrounding the eyes, and very fine streaking on the breast, indicating it is likely a juvenile and of Antillean origin. The third owl was photographed by Paul Cavanagh on Bottle Key, in northeast Florida Bay, on 24 August 1987. His photographs show the characteristic unstreaked back and lightly streaked belly of Antillean birds. The fourth owl, photographed by Hoffman at Ft. Zachary Taylor, Key West on 4 April 1994, also shows the unstreaked back, lightly streaked belly, and the sparsely feathered feet of Antillean birds, as well as the black feathering around the eyes seen on the five presumed juvenile male specimens. The fifth owl is the first of seeming Antillean origin found north of southernmost Florida. The bird was rescued from the surface of the Gulf of Mexico about 110 km west of Hernando Co (northwest of St. Petersburg) in early June 1994. It was photographed, rehabilitated, and eventually released by the Birds of Prey Center of the Florida Audubon Society. The sixth owl was photographed 29 April 1997 on Garden Key, Dry Tortugas, by Darlene Friedman and the photograph was forwarded to us by Paul Lehman; it also appears to be Antillean. We suspect that most of the other recent reports from the Florida Keys and Dry Tortugas also are of Antillean birds. Descriptions from the observers generally support this contention. Table 1 includes one *A. f. flammeus* specimen (collected 10 December 1992) and two sightings that may belong to this race (24 November 1979, winter 1983–84).

DISCUSSION

We document the occurrence in southern Florida of representatives of a population of the Short-eared Owl previously unrecorded from the North American continent. The documentation includes eight specimens and numerous photographs of several birds. The only taxon of this species previously known to occur on the continent is the Holarctic nominate race *Asio flammeus flammeus.*

Based on the characteristics of the specimens now available, we are confident that these owls are from the Greater Antilles. On geographical and historical grounds they most likely come from Cuba. Seven of our specimens, and perhaps most of the other southern Florida birds, appear to be juveniles and to have arrived during post-fledging dispersal. Breeding by Short-eared Owls is known to occur in Hispaniola and Cuba during northern hemisphere winter. Albert Schwartz collected nestlings in the Dominican Republic in November (LSUMZ 142354 and 142355), and Garrido (1984) reported a nest with eggs in Cuba on 8 December. Based on seasonality of reports, this pattern of dispersal to southern

Florida appears to be quite recent, beginning in the late 1970s.

Nomenclature of Antillean Short-eared Owls.—Assigning a scientific name to the owls invading southern Florida is a problem because the nomenclature of the Antillean Short-eared Owl is confused and poorly documented. Briefly the history is as follows. Muller (1776, reviewed in Wetmore 1928) described an owl from Hispaniola, based on Buffon (1770), as *Strix domingensis.* Subsequent authors ignored this taxon, or assumed it was based on the Burrowing Owl (*Athene cunicularia*) until Wetmore (1928) examined one short-eared owl each from the Dominican Republic and Haiti, and concluded these were examples of the subject of Buffon's illustration and account. However, prior to Wetmore's work, Ridgway (1882) described similar owls from Puerto Rico as *Asio portoricensis.* Wetmore (1928) compared his two specimens from Hispaniola to five from Puerto Rico, and concluded that those from Hispaniola were only subspecifically distinguishable from the Puerto Rican specimens. He used the names *Asio domingensis domingensis* and *A. d. portoricensis,* respectively. We find no publication that proposes and explains the merger of these taxa into *Asio flammeus.* Although Wetmore and Lincoln (1933) treated *domingensis* as a distinct species, only three years later Bond (1936), without explanation, listed these Antillean owls as subspecies of *A. flammeus.* This treatment seems to have been followed by most subsequent authors including Peters (1940). The situation is further confused because some recent authors have grouped the Hispaniolan (*domingensis*) and Puerto Rican (*portoricensis*) populations together, also without comment. Voous (1988) and Holt and Leasure (1993), for example, referred to all Antillean Short-eared Owls as the race *portoricensis* of *A. flammeus* despite the fact that the name *domingensis* seemingly has priority over *portoricensis* (Wetmore 1928). The existence of a Cuban breeding population has been recognized only since 1981, and no formal determinations of its taxonomic status have been published. Pending further study, we recommend using the single epithet *domingensis* for all the Antillean populations; Wetmore's (1928) justification for maintaining *portoricensis* separate from *domingensis* seems insufficient given his sample sizes.

We feel that the systematics and nomenclature of the Short-eared Owl are in need of revision. The validity of several races is inadequately established, in South America as well as in the West Indies. We also suspect that *Asio flammeus* may deserve splitting into two or more species. Ideally, such a revision would include detailed analyses of vocalizations, as well as studies of molecular genetic differences. The West Indian birds are among the most distinctive in plumage and structure, but the Galapagos race and the South American populations could plausibly deserve species status as well.

Biogeographic considerations.—The recent occurrence and increasing frequency of these owls in Florida raises the possibility of a new, northward colonization from the Antilles. Owls that reach mainland Florida may find habitat suitable for nesting. Nesting habitat in Cuba apparently includes pasturelands, rice fields (Garrido 1984), and sugar cane plantations (Garrido, pers. comm.). Habitats similar to all of these occur extensively in southern Florida.

If these Antillean owls colonize southern Florida, they will be part of an ongoing wave of colonizations from the West Indies. When Howell's *Florida Bird Life* was published (Howell 1932), the breeding landbird fauna of southern Florida contained only five species' populations clearly of West Indian origin: White-crowned Pigeon (*Columba leucocephala*), (Cuban) Mourning Dove (*Zenaida m. macroura*), Mangrove Cuckoo (*Coccyzus minor*), Gray Kingbird (*Tyrannus dominicensis*), and Black-whiskered Vireo (*Vireo altiloquus*). Robertson and Kushlan (1984), in their insightful analysis of the southern Florida avifauna, considered all these to be quite recent immigrants, in part because none showed geographic variation in Florida. A sixth and seventh species, Zenaida Dove (*Zenaida aurita*) and Key West Quail-Dove (*Geotrygon chrysia*), were reported breeding in the Florida Keys prior to 1850, but both now occur only as vagrants.

Since 1932 southern Florida has experienced an average of about one natural landbird invasion per decade from the West Indies. These recent immigrants are Smooth-billed

Ani (*Crotophaga ani;* Sprunt, A. Jr. 1939, 1954), Cuban Yellow Warbler (*Dendroica petechia gundlachi;* Greene 1942), Antillean Nighthawk (*Chordeiles gundlachii;* Greene 1943), Fulvous Whistling-Duck (*Dendrocygna bicolor;* reviewed by Palmer 1976, Turnbull et al. 1989), Cave Swallow [*Hirundo fulva cavicola* (= *H. f. fulva?*); Smith et al. 1988], and Shiny Cowbird (*Molothrus bonairiensis;* Smith and Sprunt 1987).

Most of these invading species had been known as vagrants to southern Florida for some time, and reports became increasingly frequent before breeding in Florida was documented. This fits a general, but often overlooked rule: range expansion tends to be driven by population dynamics (often population increases) in the source areas, rather than by habitat changes or initial reproductive success in the colonized areas.

Several West Indian birds, in addition to these owls, seem poised to invade Florida from the south or east (Bahamas). La Sagra's Flycatcher (*Myiarchus sagrae;* Smith and Evered 1992), Bahama Mockingbird (*Mimus gundlachii*), and Thick-billed Vireo (*Vireo crassirostris*; Smith et al. 1990) seem to be increasing in frequency as vagrants. Pearly-eyed Thrasher (*Margarops fuscatus*) has not been documented in North America as of this writing, but it has been extending its range northward in the Bahamas in recent years and could begin appearing in Florida in the near future. The Cuban subspecies of American Kestrel (*Falco sparverius sparveroides*) also has been expanding its range in the Bahamas, and recently was photographed by WH at Key West. Robertson and Kushlan (1984:226) speculated on potential immigrant West Indian species, naming "the Masked Duck, a hummingbird, Bahama [*Tachycineta cyaneoviridis*] and Cave swallows, Bananaquit [*Coereba flaveola*], Stripe-headed Tanager [*Spindalis zena*] and Black-faced Grassquit [*Tiaris bicolor*]" most likely. Of these, the Cave Swallow and possibly the Masked Duck (Bowman 1995) already have colonized.

The rate of immigration in recent decades, then, must be much higher than the overall post-Pleistocene rate, unless prehistoric extinction rates for immigrant populations were extremely high. The Zenaida Dove and Key West Quail Dove, once reported to breed in the Florida Keys, no longer do so. These possible extirpations of breeding populations most likely resulted from hunting and habitat destruction (Robertson 1978a, 1978b; Robertson and Woolfenden 1992).

The apparent increase in immigration rates from the West Indies to Florida may have resulted from anthropogenic changes in the environment, both in the West Indies and in Florida. Habitat changes, associated with forest clearing for grazing, cultivation, and urban development, and global climate changes are two nonexclusive anthropogenic changes to the regional environments that could drive these colonizations. All the known Cave Swallow colonies in Florida, for example, are located on concrete bridges and overpasses along highways (Smith et al. 1988), so the increase in numbers of vagrants prior to colony establishment (Robertson and Woolfenden 1992) must have reflected population or habitat changes in Cuba.

Explanations for northward colonization involving global climate change potentially can explain both the recent wave of colonizations and the dearth of West Indian birds in the southern Florida avifauna prior to this century. A global warming trend has been underway since the end of the "Little Ice Age" in about 1870 (Pielou 1991), a trend that has accelerated because of increases in atmospheric carbon dioxide, methane, and other greenhouse gasses (Maul 1989). Some West Indian birds may have colonized the Florida peninsula previously during the Holocene, but stopped during the "Little Ice Age". Although records are inadequate or nonexistent, the lower average temperatures of the "Little Ice Age" likely were manifested in southern Florida by more frequent and more severe episodes of cold winter weather rather than by cooler summer weather. These hypothetical cold episodes could have been particularly damaging to West Indian bird populations attempting to persist in southern Florida. The current warming trend also may be fueling population increases in the West Indies for the species that have recently colonized, or are appearing more frequently as vagrants. This warming trend also may be making southern Florida habitats subtly more suitable for these birds (Robertson and Kushlan 1984).

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WITHIN- AND BETWEEN-YEAR DISPERSAL OF AMERICAN AVOCETS AMONG MULTIPLE WESTERN GREAT BASIN WETLANDS

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ABSTRACT.—Connectivity of discrete habitat patches may be described in terms of the movements of individual organisms among such patches. To examine connectivity of widely dispersed alkali lake systems, we recorded post-breeding and subsequent breeding locations of color-banded American Avocets (*Recurvirostra americana*) in the western U.S. Great Basin, from 1995–1997. Among individuals observed during the post-breeding/premigratory season, over half of the 188 breeding adults were observed at lakes other than their breeding locations, whereas 70% of 125 post-fledged young were observed only at their natal lake systems. Of 46 breeding adults observed in consecutive years, only eight (17%) dispersed between different lake systems. Only 8% of chicks were observed after their first year, and only 1.3% returned to the natal area in subsequent breeding seasons. Adult and recently fledged birds from the southernmost breeding site were regularly observed in post-breeding aggregations at lakes several hundred kilometers to the north, suggesting seasonal differences in habitat quality at the lake systems studied. These results indicate the importance of maintaining habitat for post-breeding movements. *Received 10 Dec. 1998, accepted 3 April 1999.*

Concurrent with the recognition that habitat fragmentation is a key threat to regional biodiversity, the role of dispersal in maintaining connectivity between populations and subpopulations has become a major focus in assessing extinction risks and other dynamics of populations and communities (Saunders et al. 1991, McPeek and Holt 1992, Taylor et al. 1993, Dunning et al. 1995, With et al. 1997, Haig et al. 1998). For vertebrate populations, dispersal studies generally have focused upon movements within contiguous habitats or among adjacent patches. Although appropriate for some species, this approach fails to account for a significant proportion of dispersal events among more mobile species, especially those that inhabit discrete, widely-dispersed patches of habitat. In addition, connectivity measures require monitoring of multiple sites as both potential sources and recipients of dispersers. Such interchange among patches has been incorporated to varying degrees into numerous spatial models of populations (see Doebeli and Ruxton 1997, Ims and Yoccoz 1997, Wiens 1997), but empirical measures of such rates of exchange are often difficult to determine for vertebrate metapopulations.

Specifically, studies of avian dispersal are largely limited by the spatial scale that researchers are able to effectively monitor dispersing individuals and by a traditional focus on return rates rather than on broader dispersal patterns. Typically, such studies focus on a population inhabiting a single site or a few neighboring areas, with the probabilities of detection for dispersers decreasing geometrically with distance from the point of origin (Barrowclough 1978, Cunningham 1986).

To determine large-scale connectivity patterns among discrete wetlands of the western Great Basin, we examined movements of banded American Avocets (*Recurvirostra americana*) among major lake systems of an otherwise arid region. In addition to monitoring dispersal in relation to breeding sites, we also examined premigratory movements of individuals, an often neglected aspect of individual life histories that may be a critical connective element of patchy landscapes (Haig et al. 1998).

METHODS

From 1995 to 1997, we color-banded and observed American Avocets at four major alkali lake systems in high desert regions of the western Great Basin: Summer Lake and Lake Abert in Lake County, Oregon; Goose Lake in Lake County, Oregon and Modoc County, California; and Honey Lake in Lassen County, California (Fig. 1). Interlake distances range from 45–315 km. Avocet breeding locations in the region, other than our study areas, were scarce during the years of the study; although additional local breeding popula-

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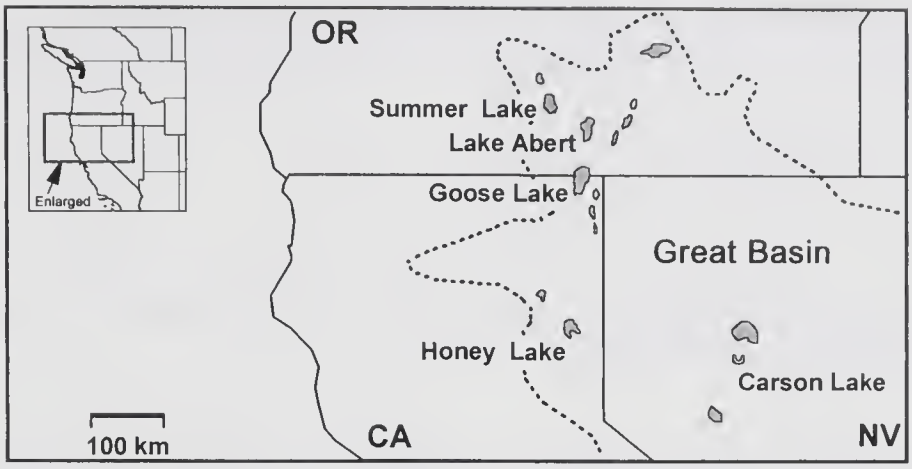

FIG. 1. Avocet study areas of the western Great Basin.

tions occur sporadically in response to suitable water conditions (Neel and Henry 1996; Oring and Reed 1996; L. W. O., pers. observ.). During breeding periods, our efforts at Summer Lake and Honey Lake were focused on managed wetlands adjacent to the main lake bodies: the Summer Lake Wildlife Area (SLWA) and Jay Dow, Sr. Wetlands (JDW), respectively, although we also conducted regular surveys along the entire lake shorelines.

During the three breeding seasons, 339 incubating adults were captured at nests and given unique combinations of color bands. Recently hatched chicks (n = 457) and flightless fledglings (n = 19) were captured and individually marked opportunistically near nesting areas. In 1995, an additional 61 individuals in post-breeding flocks were captured and banded at Summer Lake. All birds were given U.S.D.I. numbered aluminum and celluloid or Darvic™ plastic leg bands. In 1996 and 1997, radio transmitters were attached to aluminum leg bands and placed on 185 adult avocets, distributed among the four lake systems (Plissner et al. in press). Hatch-year birds were given brood-specific band combinations, with individuals identified by colored plastic tape wrapped around the numbered aluminum band. Sexes of adults were distinguished by relative bill curvature (Hamilton 1975) whenever possible but were deferred to judgments during banding in cases of conflict with observations of resighted individuals.

Banded avocets were resighted during the breeding and post-breeding periods at each lake, from April through September of each year. The Summer Lake WA and Jay Dow, Sr. Wetlands were surveyed weekly throughout the field season. Because of difficulties in accessing most of the lakeshores, the four main lakes were surveyed less frequently by foot and from vehicles and hovercraft. In 1996 and 1997, complete surveys of the three Oregon lakes were conducted weekly during the breeding and post-breeding periods. Aerial surveys and previous monitoring efforts at Honey Lake indicated relatively little use of the main lake body by avocets throughout the breeding and post-breeding periods (L.W.O., unpubl. data). Nevertheless, focal lake sites in proximity to Jay Dow, Sr. Wetlands were regularly surveyed. Observers recorded band combinations observed with 20–60× telescopes. Breeding status was assigned to birds observed at nests or in the presence of young chicks. As a conservative measure, only birds observed after 1 August were assumed to be post-breeding. We use the term "dispersal" to refer to movements between different lake systems; whereas we refer to birds returning to the same lake system as "philopatric". We also report anecdotal observations of banded avocets from wintering areas in California.

Resightings were subsequently screened against lists of known band combinations. Because of occasional band loss and the fact that some pairs of band colors became difficult to distinguish as they faded over time (Robinson and Oring 1997a), alternatives were considered for those observations that did not correspond to known combinations. If only a single alternative combination existed, the sighting was retained in the dataset. Other observations were discarded. Observations of individuals breeding in different years (bird-years) were considered independent for all summaries and analyses. Frequency data were analyzed using G-tests with Williams correction (Excel macro based on Sokal and Rohlf 1981).

RESULTS

Within year movements.—During the study period, we monitored postfledging/postbreeding movements for 476 hatch-year and 339 breeding adult American Avocets (151 females, 170 males, 18 unknown gender) banded in the western Great Basin. One bird, originally banded as a chick, was subsequently recaptured and rebanded as a nesting adult. Eight individuals were observed at nests during two breeding seasons. Of the total monitored, 125 chicks (26%) and 188 adults (55%) observed during nesting periods were resighted during the subsequent post-fledging/post-breeding periods (i.e., after 1 August). Among

TABLE 1. Post-breeding locations of adult American Avocets in the western Great Basin, 1995–1997.

Breeding location	Adults monitored[a]	Post-breeding location[b]			
		Honey Lake	Goose Lake	Lake Abert	Summer Lake
Honey Lake	105	12	2	10	9
Goose Lake	57	0	17	11	12
Lake Abert	50	0	5	16	12
Summer Lake	133	0	4	42	62

[a] Includes seven individuals observed at nests during two breeding seasons.
[b] Multiple post-breeding locations included for 30 individuals.

adults resighted during the post-breeding period, 53% were observed at lakes other than where they had bred (Table 1). There was no significant difference in proportions of males (53.5%, $n = 99$) and females (52.6%, $n = 76$) that dispersed from breeding locations to other lake systems ($G_w = 0.014$, $P > 0.05$). Furthermore, of observed post-fledged young, 30% (38 of 125) were resighted away from their natal lake systems (Table 2), a significant difference from the adult rates of post-breeding dispersal ($G_w = 15.59$, $P < 0.05$). Five chicks and 16 adult breeders dispersed following fledging or breeding from Honey Lake to post-breeding locations among the northern three lakes, while no birds from the northern three lakes were observed postbreeding/post-fledging at Honey Lake. Four chicks and three adults were reported from wintering areas along the northern California coast (Humboldt Bay and San Francisco Bay) after leaving Goose Lake and Honey Lake natal/breeding areas. Prior to being reported on the wintering grounds, all seven birds were observed on at least one of the three Oregon lakes during the post-breeding period.

Between-year movements.—We monitored between-year dispersal locations for 454 chicks and 259 adult American Avocets (137 females, 122 males). Altogether, 197 birds were observed in the region in multiple years, including 51% of all banded adults and 8% of chicks. Of 46 adults that were observed in the region in consecutive breeding seasons, 38 (83%) returned to the same lake. Eight additional adults that bred at Honey Lake in 1995 were not observed the following year but returned to breed in 1997. Overall, return rates for chicks were 0.4% for birds observed in their first post-natal breeding period (i.e., at age 1) and 1.3% for birds observed during their first two post-natal breeding seasons (i.e., ages 1 or 2). Of eleven banded chicks resighted during subsequent breeding seasons, seven (64%) returned to the natal lake system. The other four chicks, all banded at Honey Lake, dispersed to Oregon lakes in subsequent breeding seasons. No adults dispersed from Honey Lake to the northern lakes between years, and no birds of any age class from Goose, Abert, or Summer Lakes dispersed south to Honey Lake during subsequent breeding periods. Four birds (three males and one female) were observed during the breeding period of all three study years. Three of the four were observed at Honey Lake during all three years. The other individual bred at Summer Lake in 1995 and 1996 and was observed at Lake Abert during the breeding period in 1997. Only four individuals that bred in 1996 and 1997 were observed during the post-breeding period of the previous year. One of the four nested in 1997 at Summer Lake after nesting and spending the post-breeding

TABLE 2. Post-fledging locations of American Avocets in the western Great Basin, 1995–1997.

Natal location	Chicks monitored	Post-fledging location			
		Honey Lake	Goose Lake	Lake Abert	Summer Lake
Honey Lake	201	21	0	6	2
Goose Lake	169	0	45	12	14
Lake Abert	10	0	0	5	1
Summer Lake	97	0	1	2	16

period at Lake Abert in 1996. The other three bred and spent the post-breeding period at the same lake in both years.

DISCUSSION

Our results demonstrate within and between year patterns of dispersal at a regional scale. Earlier studies of movement patterns of avocets and other recurvirostrids focused on rates of philopatry and dispersal of individuals within a single wetland (Cadbury and Olney 1978, Watier and Fournier 1980, Sordahl 1984, Cadbury et al. 1989, James 1995, Robinson and Oring 1997b) or relied upon occasional surveys and anecdotal reports of marked individuals from areas away from the study area (Robinson and Oring 1996). By regularly monitoring birds at multiple, distant lake systems, we were better able to define the movement patterns and extent of movements at a scale more appropriate to the life history of the species. Still, we recognize the fact that, in order to gain an objective measure of dispersal, monitoring of more distant sites in multiple directions from breeding areas would be required.

Return rates of individuals we observed differed somewhat from those described for avocets in an earlier Great Basin study at Honey Lake, California. Robinson and Oring (1997b) estimated that 21–25% of avocets chicks that were known to have survived to breeding age returned to the natal site to breed, whereas we observed 64% of known survivors (i.e., individuals observed after their hatch-year) returning to the natal lake system. In relation to the total number of chicks banded, however, our return rates were lower (4.2%, Robinson and Oring 1997b; 1.3%, this study), suggesting that survivorship of chicks was likely the distinguishing variable. Return rates of breeding adults were significantly different in the two studies (24%, Robinson and Oring 1997b; 18%, this study; $G_w = 4.24$, $P < 0.05$). Relative to other species of Charadriiformes (Oring and Lank 1984), natal and breeding philopatry rates of avocets in the western Great Basin were low, perhaps resulting from the extensive annual variability in breeding habitat suitability.

The small number of interlake breeding and natal dispersal events during the three years of the study suggests limited, but adequate (Wright 1951), gene flow among Great Basin breeding populations. Furthermore, the pattern of both post-breeding and between year dispersal suggests an unbalanced pattern of connectivity, perhaps indicative of source-sink metapopulation dynamics (Pulliam 1988), with Honey Lake/Jay Dow, Sr. Wetlands serving as a source population in relation to the three Oregon lakes. This hypothesis is further supported by observations that productivity at Jay Dow, Sr. Wetlands has generally been higher than at the other study areas (S.M.H. and L.W.O., unpubl. data). Historically, in a system with high interannual variability in habitat patch quality resulting from fluctuations in precipitation (Engilis and Reid 1997, Robinson and Warnock 1997), sources and sinks may have shifted periodically. Such shifts would characterize a rescue effect metapopulation (Brown and Kodric-Brown 1977), in which local populations, in danger of extinction if isolated, nevertheless persist as their numbers are buffered by immigration from populations with more favorable breeding conditions (Stacey et al. 1997). As a recently developed, managed wetland, the Jay Dow, Sr. Wetlands may in fact now be a stable source for avocet populations at other wetland systems throughout the western Great Basin.

Post-breeding movements also suggested seasonal differences in the use of various wetlands within the region. Primary breeding areas such as the managed wetlands (Jay Dow, Sr. Wetlands and Summer Lake WA) were relatively less important as post-breeding habitats, whereas the major lake bodies, particularly the three northern waterbodies in our study (Goose Lake, Lake Abert, and Summer Lake), supported much higher densities of birds in late summer and early fall than during the breeding season (Warnock et al. 1998). Our observations of post-breeding dispersal from Honey Lake to northern lakes may reflect differential habitat suitability of the lake systems during this time period. Avocets from Honey Lake also have been reported in post-breeding flocks at water bodies east and south of the breeding/natal lake system (Robinson and Oring 1996, 1997b; Plissner et al. in press); indicating a multidirectional exodus from this particular breeding area in late summer and early fall. As an alternative to hypotheses of seasonal resource tracking, other

studies have suggested that premigratory movements of birds are exploratory or otherwise associated with identification of future breeding areas (Morton et al. 1991, Reed and Oring 1992, Reed et al. in press). Our results, however, do not provide evidence for associations between post-breeding locations and subsequent nest sites, as would be expected for support of this hypothesis.

The observed patterns of dispersal movements were confirmed by radio telemetry data (Plissner et al. in press), which also demonstrated a northerly trend in post-breeding movements of avocets between Carson Lake, Churchill County, Nevada (Fig. 1) and the three Oregon lakes of this study, without evidence of southward post-breeding movements by Oregon breeders. Telemetry data further indicated that a very high proportion of post-breeding adults (71%) frequented wetlands other than their breeding locations. In addition, radio-tagged individuals frequently were not detected at any of the primary lakes during some telemetry surveys, suggesting even greater rates of movements away from breeding locations during the time period. Therefore it is likely that visual resightings of individuals represent a conservative estimate of the extent of post-breeding movements in the region. Nevertheless, these data provided information on movements across multiple years and for first-year birds, which can not be obtained effectively using current telemetry methodologies.

Post-breeding locations may also be associated with specific migration routes and/or wintering areas for these populations. All birds reported during the fall/winter along the northern California coast, including those originating from Honey Lake, were last observed at one of the three northern lakes. Previous reports suggest that birds originating from Honey Lake primarily migrate to wintering areas in California's Central Valley and coastal areas from San Francisco Bay south to the central coast of Sinaloa, Mexico (Robinson and Oring 1996, Robinson et al. 1997). Numbers of avocets at the northern extreme of the species' winter range (Humboldt Bay, California), however, have been increasing since 1960 (Evans and Harris 1994), and it is clear that many of these birds originated from breeding areas throughout the western Great Basin. Although further data are needed from other wintering areas, it appears possible that birds that aggregate at post-breeding areas in the northwestern Great Basin may overwinter along the northern California coast, whereas others, even from the same breeding area, may migrate directly south and west to more southerly post-breeding and wintering sites.

Our studies of American Avocet movements in the western Great Basin indicate that a dispersal-based evaluation of habitat connectivity requires an understanding of movements at multiple temporal and spatial scales. Based solely upon movements of individuals between breeding sites, connectivity among the different wetlands of the region would appear to be weak. Rates of post-breeding movements among different lake systems, however, was substantially higher, providing evidence of a strong link between the different systems. An apparent northward trend in long-distance post-breeding dispersal suggests that the northern lake systems may provide better resources for avocets during this time period, while the same trend in between-year movements may be simply a geographic artifact of the location of a source population relative to other study populations with lower productivity. This hypothesis also is supported by observations of avocets from Jay Dow, Sr. Wetland at stopover areas farther south (Robinson and Oring 1996), suggesting a multi-directional exodus of post-breeding birds from Honey Lake breeding sites. Thus, avocets use a large array of Great Basin wetlands within and among years, suggesting that conservation efforts should consider this complexity in defining appropriate habitat conservation strategies.

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HIGH MORTALITY OF PIPING PLOVERS ON BEACHES WITH ABUNDANT GHOST CRABS: CORRELATION, NOT CAUSATION

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ABSTRACT.—Ghost crabs (*Ocypode quadrata*) have been implicated in mortality of eggs and chicks of the beach-nesting Piping Plover (*Charadrius melodus*) whose Atlantic Coast populations are listed as threatened. Through observation and experimentation, we investigated the interactions between ghost crabs and plovers on Wild Beach, a Piping Plover nesting area on Assateague Island, Virginia. This site has a high abundance of ghost crabs and historically low fledging success compared to adjacent areas with fewer crabs. We observed encounters of crabs with plover eggs, chicks, and adults in the field, but never predation. In staged encounters of crabs with eggs and chicks (using hatchery reared quail as plover surrogates), we were unable to elicit predatory behavior either on the beach or in the lab. We conclude that although instances of ghost crab predation on Piping Plover eggs and chicks occur, they are rare and cannot account for the high mortality frequently reported on beaches where ghost crabs are abundant. Adult plovers behave toward crabs as if they were dangerous to eggs and chicks, and their young broods in the study area did not forage along the foreshore. Hence, ghost crabs may increase mortality indirectly. Frequent responding to crabs by parents may attract more deadly brood predators. Brood nutrition may suffer as adult plovers direct chicks away from areas where forage is reportedly richer but crabs are abundant, such as the foreshore. Nutrient intake may be further reduced on more southerly breeding grounds where high temperatures on backshores force chicks to stop foraging and take shelter during mid-day. Although high mortality cannot be attributed directly to predation by crabs, it may be due to factors that covary with crab abundance, such as high temperature, behavioral responses of adult birds, and poor forage. *Received 28 April 1998, accepted 7 Feb. 1999.*

Anecdotal and published reports of ghost crab predation on Piping Plovers (*Charadrius melodus*; Loegering et al. 1995, Watts and Bradshaw 1995) have led to concern that crab predation may hamper recovery of plovers on the Atlantic Coast, where the species is listed as threatened (Loegering and Fraser 1995; U.S. Fish and Wildlife Service 1993, 1996). To assess the extent of crab-caused mortality, we investigated interactions between ghost crabs (*Ocypode quadrata)* and Piping Plovers during incubation and chick rearing on Wild Beach on Assateague Island, Virginia, within the Chincoteague National Wildlife Refuge. Compared to other portions of this barrier island that are used for nesting areas by the Piping Plover, Wild Beach has higher abundances of ghost crabs (Britton 1979) and lower rates of fledging success (U.S. Fish and Wildlife Service 1994).

Piping Plovers breed from eastern Canada to North Carolina, as well as in the Great Lakes region and the Great Plains of Canada and the U.S. (Haig 1992). On the Atlantic Coast, plovers typically lay four eggs in a shallow scrape in the sand, usually well beyond the high-tide mark, or in shelly storm-flattened areas (washouts) between and behind the primary dunes. Chicks are precocial and forage in moist backshore areas where available, or on the foreshore (the area between the tides; Loegering and Fraser 1995).

Ghost crabs, named for their cryptic coloration, range along the Atlantic Coast from Rhode Island to Brazil and throughout the Caribbean (Chace and Hobbs 1969). They are among the fastest terrestrial invertebrates (Full and Weinstein 1992) and formidable predators with acute sensory receptors for vision, vibration, taste, and smell (Cowles 1908, Wellins et al. 1989). They are most abundant on high energy beaches, where they obtain over 90% of their diet preying on intertidal invertebrates (Wolcott 1978). They are extremely flexible foragers, also scavenging, deposit feeding, consuming seeds and insects, and are documented predators of turtle hatchlings (Arndt 1994, Robertson and Pfeiffer 1982). At dusk crabs move from their burrows on the backshore and among the dunes to feed in the swash zone. Crabs seek out and take refuge in burrows as dawn approaches (Wolcott 1978).

Poor fledging success on beaches where crabs are abundant, coupled with extensive

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seasonal and spatial overlap between plovers and the predatory ghost crabs, led to the hypothesis that ghost crab predation is a common source of mortality for plover eggs and chicks (U.S. Fish and Wildlife 1993, Loegering and Fraser 1995). To test this hypothesis, we documented and quantified natural encounters between crabs and Piping Plover eggs and chicks, and staged encounters between crabs and the eggs and chicks of nonthreatened species.

METHODS

We conducted our study on a 6.4 km stretch of the Chincoteague National Wildlife Refuge's (NWR) Wild Beach, Virginia, in June and July, 1994. Wild Beach has a steeply-sloped foreshore rising from a high energy surf zone to the berm and was characterized in 1994 by one or two wave-cut scarps less than 1 m high. At the berm the slope decreased abruptly and there was a narrow (20–50 m), flat backshore region. Inland of the backshore are low vegetated foredunes, fronting 2–4 m high artificially stabilized dunes vegetated with beach grass (*Ammophila breviligulata)* and seaside goldenrod (*Solidago sempervirens).*

We observed four natural plover nests through the last days of incubation and past hatching using continuous video monitoring to document crab predation on eggs and newly hatched chicks. When the third egg was laid in each nest, staff from the refuge surrounded the nest with a 4 m diameter, 1.5 m high exclosure constructed of 5 × 10 cm welded mesh wire supported by reinforcing bar and covered with plastic netting. A dummy camera was mounted at the top of an exclosure support bar on the southwest side, facing toward the nest and away from the prevailing wind. At the time nest observation began, the dummy camera was replaced with a similar appearing video surveillance camera fitted with infrared light-emitting diodes for nocturnal illumination, and an infrared filter to prevent saturation in strong sunlight. The camera imaged an area approximately 2 × 3 m centered on the nest. Installing the camera in place of the dummy took 3–12 min, and birds returned to the exclosure 1–9 min thereafter (mean = 4.25 min., $n = 4$). Coaxial and power cables (150 m) led to a TV/VCR (Magnavox model CCR095) powered by a deep-cycle lead-acid battery. These were housed in a tent behind nearby dunes to reduce disturbance to the plovers. Tapes were changed at six-hour intervals and the battery every 18 hours. According to the video record, the incubating adult plovers typically did not flush from the nest at those times. Video tapes were reviewed for the following occurrences and the times logged: adult plover brooding, alarming and flushing from the nest (rapid rising off eggs, standing near nest with wing raises, rapid exit from the field of view), parental exchanges of incubating/brooding duty (second parent appears on screen and changes places with the bird on the nest), eggs hatching, activities of chicks (including walking, foraging and being brooded), and any activities of ghost crabs.

To explore the role of crab predation after chicks left the nest, we observed encounters between crabs and adult plovers and chicks for eight days, concentrating on periods of peak crab activity. Observations of hatched broods were made from a vehicle at least 30 m away, using binoculars during daylight hours, and an image-intensifying scope (Varo Noctron IV) at night fitted with an infrared diode laser to enhance illumination. Plover chicks in two broods were marked on each thigh with 10 mm diameter disks of Scotchlite™ (3M) reflectorized tape glued to the surface of their down to make them visible with night vision equipment. Two of the marked chicks were the only chicks to fledge in the study area; thus the treatment did not appear to increase mortality. Data collected during each observation period included the location of the brood, the place and time spent foraging, and the location of brooding.

To further assess the probability of ghost crabs preying on eggs, we presented crabs with surrogate eggs that were similar in size and shape to those of *Charadrius melodus* (see MacIvor et. al. 1990). Japanese Quail (*Coturnix japonicus)* eggs were obtained from a local bird breeder, and Northern Bobwhite (*Colinus virginianus*) eggs were obtained from Seven Oaks Game Farm and Supply, Wilmington, North Carolina. On three nights, we constructed four scrapes near the berm and placed four *Coturnix* eggs in each just prior to the time that crabs emerge from their burrows. During the nocturnal peak in crab activity (19:30–22:00 EST), the artificial nests were observed for any ghost crab encounters using the video camera unit fixed on a tripod.

To further explore the vulnerability of eggs to ghost crab predation, we placed four opaque gray plastic bins (38L × 18W × 11D cm) in a rectangular array in the laboratory and filled them to a depth of about 3 cm with damp sand from the foreshore. In each we placed a ghost crab [average weight 49.0 ± 5.4 (SD) g, with a carapace width of 43.2 ± 1.6 mm, $n = 8$] freshly-collected from the foreshore of Wild Beach, two *Coturnix* eggs, and the bins were covered with chicken wire. Crab activity was recorded using the infrared camera and VCR from the initiation of the experiment at 23:15 until 05:15, and condition of the eggs was assessed at 10:00. The experiment was repeated using dry beach sand and *Colinus* eggs on another night, and condition of the eggs assessed after 11 hours of exposure to the crabs. From the video tapes we noted the length of time crabs spent in contact with eggs, their behavior, and the condition of the eggs after manipulation by the crabs.

To elucidate potential predatory interactions between crabs and chicks, we used chicks of Northern Bobwhite as surrogates for Piping Plover chicks. Bobwhite chicks are similar in size and behavior to Piping Plover chicks, but darker and hence less cryptic on beach sand. Two- and three-day-old chicks ($n = 14$)

were released near the beach berm into areas of high crab activity to maximize encounters with crabs and were observed with binoculars as they wandered on the beach. In four cases, chicks were deployed from the parked vehicle (to which crabs showed little response) into the immediate vicinity of active crabs. To verify that crabs were motivated to forage, we placed dead chicks, freshly cracked oysters, and pieces of thawed chicken upwind near the mouths of occupied burrows at the same time that live chicks were released onto the beach. Encounters between crabs and chicks and dead prey were documented.

To determine temporal overlap in activity between crabs and plovers, nocturnal and diurnal observations of crab activity and behavior were conducted from a vehicle. The onset of migration of crabs to the surf zone for nocturnal foraging was determined by noting the time of appearance of the first crab moving down the beach each night.

Statistics are reported as mean plus or minus one standard deviation.

RESULTS

Predation by crabs on eggs.—Ghost crabs did not prey on eggs in either natural nests or in experimental trials, and crabs showed comparable behavior toward eggs in all settings. In 147 hours of video observations of incubation by Piping Plovers, there were seven appearances of ghost crabs in the video field. These appearances generally were confined to the periods of crepuscular movement by the crabs (dawn, 04:16 ± 11.3 min, $n = 2$ and dusk, 20:01 ± 4.6 min, $n = 3$). Two exceptions occurred on one rainy day when high humidity and reduced insolation resulted in diurnal crab activity. In two cases, crabs directly contacted and manipulated the eggs in the nest cup after the incubating adult had flushed from the nest. Crabs appeared to be testing the eggs as potential prey, using chelae and mouthparts which contain dense arrays of chemoreceptors to "taste" the eggs. The durations of manipulations were 13 s and 23 s.

Crabs that contacted *Coturnix* eggs in pseudo-nests in the field either continued slowly toward the foreshore or stopped to manipulate and taste the eggs. Crabs spent more time in contact with eggs when manipulating them (17.3 ± 3.06 s, $n = 3$) than when they were not manipulating them (11.4 ± 8.4 s, $n = 5$). In one instance, a crab spent 6 minutes and 12 seconds at a pseudo-nest of *Coturnix* eggs on the beach, repeatedly tasting the eggs and rolling one egg several cm prior to moving on to the surf zone. We interpret this intense interest as a response to the bird feces present on that particular egg.

Crabs confined with *Colinus* eggs in the laboratory explored the eggs as potential prey at least once, not necessarily on the first contact, but simply walked over the eggs in other encounters. Four crabs spent an average of 12.2 s (± 8.2 s, $n = 11$), 10.6 s (± 11.2 s, $n = 8$), 6.9 s (± 6.7 s, $n = 10$), and 7.3 s (± 5.9 s, $n = 6$) on eggs per encounter. Average time of encounters in which manipulation occurred (all crabs) was 13.7 s (± 8.4 s, $n = 7$).

Potential for predation by crabs on chicks.—Three different Piping Plover broods were observed for a total of 26.2 h. A chick was seen to pass near a crab only once, and in that instance, there was no response from the crab.

After leaving the nest and exclosure, chicks were almost always found foraging in vegetated areas, principally on the low foredunes ($n = 18$). Chicks from Nest Five were found on high dunes because low foredunes were uncommon in their territory. This brood was seen once on the foreshore of Wild Beach on the day after it left the exclosure. Surviving chicks from all broods were taking 5–10 m forays away from the attending parent by 1.5 days, often in divergent directions. The attending adult was often seen following after a rapidly moving chick. Typically the attending adult stayed near the chicks, outside the vegetation, while the other adult stationed itself near the berm, standing sentinel and frequently feeding on the foreshore. During midday chicks alternated between foraging and resting in the shade of vegetation. The parent typically moved the chicks back to the same general area each evening to brood. Typical brooding areas were in shell hash (broken shell fragments) on the backshore near foredunes, a few meters from dune vegetation.

Activity periods of birds and crabs showed little overlap once the chicks left the nest. Parent birds began brooding chicks as each evening became cool, from about 18:30 to shortly before 20:00 (19:05 ± 28 min, $n = 8$), until chicks ceased making forays altogether, typically between 19:00 and 20:30 (20:00 ± 38 min, $n = 8$). First sightings of crabs moving to the foreshore occurred about the same time that chick activity fully ceased (19:51 ± 9 min, $n = 7$ nights). Crab activity increased

during the following hour, and chicks were brooded during the peak of activity. In the morning, crabs migrated from the foreshore to their burrows before dawn (04:16 ± 11.3 min, $n = 2$ mornings), and before broods were seen to become active. Some crab activity persisted throughout the day, generally restricted to the vicinity of burrows whose densities increased from the dunes toward the berm.

No instances of crab predation on bobwhite chicks occurred, although more than 30 encounters were observed in 12 hours of diurnal and nocturnal observation. In the one case in which a crab seized a quail chick that was precipitously deposited next to its burrow, the crab promptly released the chick unharmed and retreated to its burrow. Most commonly, crabs showed no response to chicks that wandered nearby within visual range. Crabs were attracted to, and fed readily on, cracked oyster and chicken during the same intervals in which chicks were presented, demonstrating the crabs' willingness to forage and feed. However, crabs routinely ignored dead quail chicks, even when they physically contacted them in the course of foraging.

Crab interactions with adult Piping Plovers.—Interactions between incubating adult Piping Plovers and approaching crabs were variable. Plovers either remained on the nest ($n = 4$) or flushed ($n = 4$). Flushing typically occurred while the crabs were further than 0.5 m from the nest cup ($n = 3$), but once not until the crab approached within 10 cm. Defensive encounters initiated by the plovers could involve both parents ($n = 2$). In the four instances in which birds responded to crabs, the minimum length of engagement in the video field was 2 min (120 ± 49 s, $n = 4$). However, adults left the nest cup unattended for about 5 min (307 ± 197 s, $n = 4$), presumably continuing the defense out of the camera's view.

Aggressive displays by incubating adult plovers against approaching crabs were largely ineffectual. Crabs generally remained motionless or maintained course ($n = 3$) when confronted by adult plovers advancing slowly with uplifted wings, but sometimes they ran when charged by a displaying bird ($n = 2$). In one instance, a crab whose course would have bypassed the nest was deflected onto the nest while veering from the displaying parent.

Thirteen encounters between crabs and adult plovers with unfledged chicks were observed, with variable behavior by the plovers. Once, an adult passed within 10 cm of a crab with no apparent response. Where interactions occurred ($n = 12$), plovers always initiated them, although the crab was 8–50 m from the brood. Plovers would approach and display within 10–20 cm of the crab. Birds were seen feigning and leading crabs toward the foreshore (max distance = 10 m, max time = 4 min, $n = 3$). Three encounters involved both parents.

Adult plovers appear to associate the presence of burrows with ghost crabs. A burrow that was near a nest was ignored for the first 85 hours of video observation, but was closely inspected by the adult plovers on 11 separate occasions in the final 11 hours of observation after a crab had approached the nest from that direction. Burrows were also investigated on the beach by parents with hatched broods ($n = 2$).

Plover behavior and mortality.—Although we observed no instances of Piping Plover mortality directly attributable to predation by ghost crabs, we documented other factors that might directly or indirectly contribute to the low fledging success on Wild Beach. Hatching asynchrony (substantial time, e.g., >24 hrs between hatching of the first and final eggs in a given clutch) was responsible for the only mortality for which a cause could be established, and the only mortality to occur prior to hatching. Hatching asynchrony showed a strong seasonal correlation in this study. Six clutches of eggs were laid on Wild Beach in 1994 (Table 1). For the two monitored broods in June, hatching was highly synchronous. The time between the hatching of the first egg and the last egg in an entire clutch averaged 104 min. In the three July broods, duration of hatching averaged at least 1680 min. The asynchrony contributed directly to the abandonment of an egg, which was determined to be viable (Refuge Staff pers. comm.).

Of 23 chicks that hatched on Wild Beach in 1994, two fledged. Half the mortality occurred in the first two days, and 75% by day five (Fig. 1). This pattern of chick loss soon after hatching is typical for the species, but even more pronounced than reported in previous studies (most mortality in the first 10

TABLE 1. Data for broods of Piping Plover (*Charadrius melodus*) hatching on Wild Beach, Assateague Island, 1994. Based on six clutches laid on Wild Beach; nests 2, 3, 5 and 6 were monitored via video camera.

	Nest 1	Nest 2	Nest 3	Nest 4	Nest 5	Nest 6
Hatch date	June 10	June 10	June 16	July 4–6	July 6/7	July 8/9
Hatch duration	?	20 min	3 hr 08 min	>36 hr	>24 hr	>24 hr
Interval to walk	?	1 hr	1–2.5 hr	?	6 hr	5 hr
Time nest abandoned	?	18:49	16:10	?	16:37	15:44–18:45
Survival, days (time of death where known[a])						
chick A	0.5 (n)	0.5 (n)	1.5	?	1–2 (d)	0.5 (n)
chick B	0.5 (n)	0.5 (n)	1.5	?	3–4 (d)	0.5–1.5 (n)
chick C	7	1 (d)	fledged	9	4 (d)	1–2
chick D	16	1.5	fledged	13	never hatched	4–5

[a] Where frequency of observation permits, the time of disappearance of chicks is given as day (d) or night (n).

days; MacIvor 1990; Patterson 1988; U.S. Fish and Wildlife Service 1993). Mortality of chicks in all the June broods was highly concentrated in the first 48 hours (67%), with 25% occurring during the first night. In the monitored July broods, mortality did not occur during the first night, but was spread rather uniformly over the first week.

We could not document the cause of mortality and the fate of "disappeared" chicks. All mortality on Wild Beach occurred after broods had left the nest. Where confirmed sightings allowed the time of disappearance of chicks to be established with some certainty, chicks were as apt to vanish during the night as during the day (Table 1). Five chicks disappeared between sunset and 09:00, and five between 08:00 and 19:00. Signs of direct predation were never found.

Differences in diel activity patterns between June and July broods were documented through video observation, and indicated differences in potential for prey acquisition and for practicing locomotor and feeding behaviors during the first day of life. Hatching was highly synchronous in June, but asynchronous in July (Table 1). Chicks emerged from the nest cup for brief excursions as soon as 1 hour after hatching in the June broods, but after 5–6 hours in the July broods (Table 1). For June broods (2 and 3), chicks spent extended periods in the shade of vegetation near the nest, or out of the camera's field of view, before returning to the brooding parent, and were active throughout the day. July chicks spent little time away from the nest and were continually brooded during the hot midday.

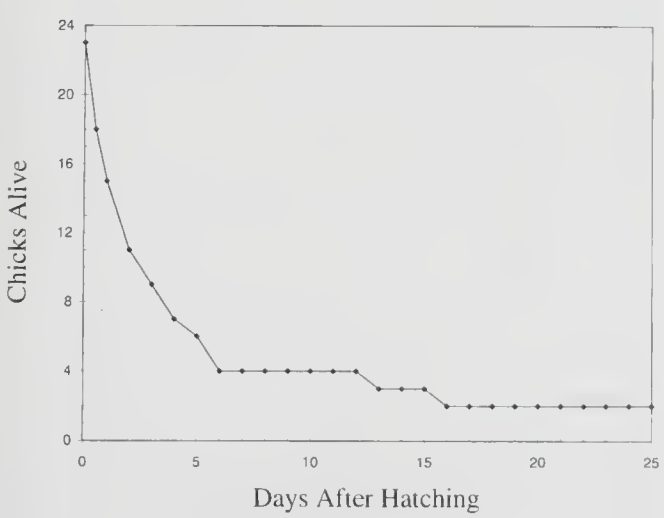

FIG. 1. Chick survival, broods 2–6.

Newly hatched chicks in all broods left the exclosure between 16:00 and 19:00 (Table 1). The chicks ranged from 4 to 12.5 hours in age, and exhibited obvious age-related differences in coordination for walking and running, both within and between broods.

Once the nest was abandoned, it was no longer possible to observe broods by using video. However, in one of the asynchronous broods, detailed observation of brooding and foraging of day-old chicks was made by video on three chicks that spent their first day post-hatch (July 7) in the area of the nest while the fourth egg was still being incubated. There was an initial peak in activity of the chicks (50% of each hour spent moving about) between 05:00 and 07:00 and another (30%) after 14:00. Activity remained below 10% between 09:00–13:00, and fell to zero at 12:00 when chicks were continuously brooded. Foraging, as seconds per hour that a chick spent

in hunt and peck behaviors, was congruent with the activity pattern (300 s/hr 05:00–07:00, <10 s/hr 11:00–12:00).

DISCUSSION

Crab predation on Piping Plover chicks.—Ghost crabs do not appear to be directly responsible for the poor breeding success of Piping Plovers on Wild Beach on Assateague Island. Ghost crabs showed no predatory response to nearby chicks of Piping Plover or Northern Bobwhite, and occasionally even ran away from chicks. Since crabs that were active during daylight hours readily fed on other prey, we conclude that chicks (at least Northern Bobwhite) are not preferred prey.

Beyond the crabs' apparent lack of interest in chicks, there is temporal and spatial separation in crab and chick activity that further reduces, but does not eliminate the likelihood of interactions. Ghost crabs are principally nocturnal; they become active after sunset and migrate to the foreshore to prey on macroinvertebrates. Crabs leave the foreshore and return to burrows by dawn. During the early morning hours, they may be active near their burrows, spending time on burrow repair, defense, and intraspecific aggression, until they are confined below the surface by microclimatic conditions. Crab activity is extended on days with low desiccation risk (pers. obs.). Although breeding adult plovers may forage extensively on the foreshore at night (Staine and Burger 1994), unfledged chicks on Wild Beach are almost entirely diurnal. During the periods when crabs are most active, chicks are being continuously brooded, at least through the first week post-hatching when most chick mortality occurs. In addition to temporal separation, spatial separation of chicks and crabs was also evident. Only once was a brood seen foraging in the intertidal prior to two weeks post-hatching; all other foraging occurred within 5 m of the dunes onto the backshore, and hence was well inland of the berm and the densest aggregation of crab burrows.

The possibility of occasional predation on foraging chicks by crabs cannot be dismissed. Only a single documented event (Loegering et al. 1995) has occurred in over 116 h of direct observation in this and other studies (Patterson 1988, 44 h; Loegering 1992, 46 h; this study, 26 h). Based on our observations, predation is most apt to occur when a chick startles a crab, especially one that has been recently defending its burrow. Aggression between crabs peaks during the early morning hours as they compete for burrows. Land crabs of several species will jump, either on potential prey, or as part of aggressive encounters (Herreid 1963, Evans et al. 1976, pers. obs.) On video we observed an hours-old plover chick careening head first into a crab burrow. Had the burrow been occupied, the chick might have been killed. Nevertheless, our data indicate that stalking and killing of chicks by crabs is highly unlikely.

Crab predation on eggs.—Video observations in our study show that ghost crabs that make contact with Piping Plover eggs investigate the eggs as potential prey items, using stereotypical tasting behaviors. Crabs showed the same behavior toward surrogate eggs of *Coturnix japonica* and *Colinus virginianus* on the beach and in the lab. However, the claws of the largest crabs on Wild Beach do not have a gape large enough to directly crush a plover egg, and no predation was observed.

Nevertheless, ghost crabs are confirmed, though infrequent, predators of Piping Plover eggs on barrier islands in Virginia (Watts and Bradshaw 1995; Refuge staff, this study) and North Carolina (S. Philhower, pers. comm.). Viable eggs have been found in crab burrows (S. Philhower, pers. comm.), but from known crab behavior and observations during this study, we conclude that ghost crabs are most likely to attack or manipulate eggs that are rotting, cracked, or dirty. Crabs use dactyls and claws for contact chemoreception, and distance olfaction to track odor plumes to the source of a smell (Wellins et al. 1989). Ghost crabs that encounter a large food parcel (e.g., a dead fish) typically dig a burrow immediately adjacent to it, which provides security for extended scavenging. Crabs that burrow next to a nest may do so because they identify plover eggs as potential food. For instance, a ghost crab burrow was found immediately adjacent to a Piping Plover nest on a beach 10 km south of Wild Beach when refuge staff inspected the nest after it was abandoned by the adults after 35 days of continuous incubation (normal development time is 27 d). The eggs were missing. Excavation of the crab burrow yielded three of the four eggs, one of

which was emitting a powerful smell. The missing egg was assumed to have been consumed by the crab. A crab that has experienced eggs as prey may subsequently recognize intact and odor-free eggs as food through non-associative learning (Evans et al. 1976). It is unclear whether broken eggs that have been found in crab burrows were already cracked, and hence emitting an attractive odor, or were cracked from hitting each other in the burrow. Whether instances of nest predation by ghost crabs were initiated as scavenging or as predation, the end result is that some viable eggs are lost to crabs. Nevertheless, we conclude that egg predation by ghost crabs cannot account for poor breeding success of Piping Plovers on Wild Beach.

Piping Plover response to crabs.—Whatever the actual threat from ghost crabs, adult Piping Plovers treat them as potential predators. We observed 16 instances in which one or both adults engaged in extensive displays against crabs, and in 5 cases, the defense left hatched broods unguarded. Further underscoring the perceived threat from crabs, adult plovers seem able to connect the presence of burrows with ghost crabs, and invest time and energy in investigating burrows.

The presence of abundant ghost crabs may create indirect problems for plovers by several mechanisms related to the adults' perception of crabs as potential predators. First, obvious responses to ghost crabs may alert truly dangerous predators, both avian and mammalian, to the location of the brood at the very time the parents are busy elsewhere and leave it undefended. Second, more frequent alarm and defense behaviors carry an energetic cost (reviewed in Walters 1984). Finally, it is possible that the abundance of crabs on the backshore induces the adult Piping Plovers to shepherd their broods away from the foreshore, where forage might be more abundant and have a higher water content. Broods elsewhere on Assateague Island are routinely taken to the foreshore (refuge staff, pers. comm.).

Given the minimal direct threat posed by ghost crabs, and the potential negative consequences of frequent display and restricted foraging, it seems maladaptive on the part of the adult Piping Plovers to treat crabs as dangerous predators. Natural selection acting on adult defensive behavior should have eliminated the behavior if ghost crabs are not significant predators and if engaging in defense towards ghost crabs increases the likelihood of predation by other predators. However, lack of sufficient genetic isolation between birds breeding in areas with and without ghost crabs would preclude such selection. Instead, some Charadriidae appear to recognize several animal categories, including avian, mammalian (with a subset of ungulate), reptilian and "other". They have evolved unique displays to each group (reviewed in Gochfield 1984). They generally distinguish potential predators from non-predators, especially among birds, thereby minimizing false alarms (Walters 1990). However, they seem less discriminating about other intruders, lumping disparate taxonomic groups into a category of "potential threat" in an "urgency of response scheme" (Walters 1990). Perhaps Piping Plovers indiscriminately categorize anything terrestrial but "neither a large mammal nor a snake", and moving near a nest or near chicks, as requiring immediate alarm. This group might include dangerous predators such as rats or mustelids to which immediate alarm would be adaptive. If one postulates that organisms such as crabs and turtles, which do not pose a significant threat but which do elicit alarm responses from parenting plovers (refuge staff, pers. obs.), are lumped into the same "dangerous predator" category in the alarm response hierarchy, the apparently maladaptive alarming by Piping Plover parents could be explained. Given the large geographic range and variety in breeding habitat, with concomitant and unpredictable variation in the suite of predators, mounting a defensive display against anything novel in the area of the brood might have at least neutral if not beneficial effects on fitness.

Correlations between low fledging success and high ghost crab abundance.—We hypothesize that high ghost crab abundance and low fledging success of Piping Plovers have a correlative, not causative, relationship. Three factors contribute to the correlation: beach and dune morphology, climate, and parental behavior.

Ghost crabs are most abundant on high energy beaches backed by high dunes. The high dunes provide overwintering habitat in which crabs are able to burrow below their lethal iso-

therm (6–8° C) before being blocked by the water table (T.G.W., unpubl. data), while high-energy beaches provide habitat for the crabs' preferred prey (Wolcott 1978). However, beaches that are backed by dunes and that lack low-lying moist habitat away from the surf, may be poorer habitat for raising Piping Plover broods, even in the absence of crabs. On Assateague Island, slower growth with concomitant reduced survival has been documented for chicks reared on an ocean beach, compared with chicks from other areas with low-lying moist habitat for foraging (Loegering and Fraser 1995). Prey abundance (measured in the wrack zone) and foraging rates were lower on the ocean beach as well. Wild Beach lacks the low-lying moist areas that are the major foraging habitat for young plover broods in the more productive breeding areas on Assateague. Even the steep intertidal with its sharp escarpments may pose a physical barrier to young broods moving to the foreshore.

During the same time as our study, over 90% of chicks successfully fledged on a site approximately 400 m inland from our site, with extensive moist low-lying forage but no access to the beach. Similarly 91% fledging success occurred on a low energy beach at the southern tip of Assateague Island, with extensive backshore foraging areas. Meanwhile less than 10% of chicks fledged on Wild Beach, a percentage similar to its long-term average (1988–1994, U.S. Fish and Wildlife 1994). Poor forage is more likely to contribute to the unusually high chick mortality on Wild Beach than direct ghost crab predation.

Climate and latitude probably play a role in the plover-crab relationship. From their northern limit in New Jersey through the southern limit of plover breeding in North Carolina, ghost crabs increase in size and abundance (U.S. Fish and Wildlife Service 1996). Presumably, at lower latitudes more adult crabs are able to successfully overwinter, emerge earlier in the spring, have a longer active season, and grow to a larger adult size. Higher abundance of large crabs leads to more encounters between birds and crabs, with an increase in adverse indirect effects on Piping Plovers.

The hotter summer temperatures associated with lower latitudes may directly affect brood survival of Piping Plovers. High daytime temperatures may speed the rate of embryo development and lead to greater hatching asynchrony (reviewed in Magrath 1990, Shields 1998). Asynchrony may contribute to mortality directly by causing abandonment of viable, late eggs, and indirectly, by reducing the cooperative attendance by adults of the hatched young. In our study, severe asynchrony also resulted in broods having chicks of very different locomotor capabilities, which could increase the likelihood that chicks will become separated from one another and lost.

Desiccation poses an even more immediate danger to the chicks. Piping Plovers acquire water from their food and thermoregulate by panting (Haig 1992). During the critical first day, broods hatching in hot weather during our study showed a reduction in foraging time and activity compared to broods hatching in cooler weather. Should heat cause a persistent shift in activity, it implies that during hot weather intake of food and its included water is lowered at the same time that evaporative losses become greater. Understanding the relationship between elevated temperatures, asynchrony, and brood survival is critical to informed management decisions at the southern end of the Piping Plover's breeding range.

The behavior of the adult plovers to the perceived threat of the crabs compounds the problem of desiccation because the adults apparently restrict their broods to the duneline, where forage is sparser and drier. On longer time scales, restricted feeding times and poor forage will result in slow growth and increased mortality (Loegering and Fraser 1995). The threat perceived by adult plovers of ghost crabs on the Wild Beach may act as a barrier between broods and the richer food resources of the foreshore.

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A TAXONOMIC STUDY OF CRESTED CARACARAS (FALCONIDAE)

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ABSTRACT.—The taxonomic status of the crested caracaras (*Caracara* spp., Falconidae) has been unsettled for many years. Current sources such as the AOU Check-list recognize a single species that includes three taxa formerly considered distinct, citing observations by Hellmayr and Conover (1949) on two specimens considered to be intermediate. We studied plumage characters and measurements of over 392 museum specimens and found no evidence of clinal change between the northern and southern continental populations. Sixteen specimens from localities near the Amazon River where these two populations sporadically meet exhibit a mosaic of plumage elements from both forms. Measurements of wing chord, bill length, and bill depth indicate that size is positively correlated with latitude north and south of the equator and that females are larger than males in the northern population. These populations do not meet in western South America. We conclude that three biological species can be identified in the crested caracaras: the insular Guadalupe Caracara (*Caracara lutosus*); and two continental species, Northern (*C. cheriway*) and Southern caracara (*C. plancus*), neither of which shows subspecific variation.
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The Florida population of the Crested Caracara (*Caracara plancus audubonii*) is considered threatened by the U.S. Fish and Wildlife Service (1987), a recognition that subjects that population to strict permit regulations and consideration for conservation efforts (Morrison 1996). Although the generic name given in the Fish and Wildlife Service listing is *Polyborus,* Banks and Dove (1992) have shown that the generic name should be *Caracara.* The threatened status, together with the uncertainty reflected by various taxonomic treatments at the species and subspecies levels, has led us to complement Morrison's (1996) detailed report by examining the taxonomy of crested caracaras throughout their range.

Ridgway (1876) treated the crested caracaras as three species in the genus *Polyborus* (now *Caracara*): *tharus* Molina, 1782 of southern South America; *cheriway* Jacquin, 1784 from northern South America to southern North America; and *lutosus* Ridgway, 1876 of Guadalupe Island, Mexico. Except for the replacement of the specific name *tharus* with the earlier *plancus* Miller, 1777 by Brabourne and Chubb (1912), an action followed by Swann (1925) and all subsequent authors, this treatment remained unchanged for three-quarters of a century. Swann (1925) thought that birds from the northern part of the range of *C. plancus* in Brazil were "more or less intermediate in appearance" between more southerly *C. plancus* and *C. cheriway,* but gave no details. Hellmayr and Conover (1949), stating that *C. cheriway* "appears to us nothing else but a well-marked race of the Southern Caracara," were the first to unite the two continental populations into a single species, *C. plancus.* The chief distinguishing characters of blacker coloration and reduction of white barring both on rump and chest were considered by Hellmayr and Conover (1949) as "merely differences of degree." They also noted that the apparent gap in measurements between extreme southern *C. plancus* (Strait of Magellan) and *C. cheriway* was bridged by specimens from intermediate localities. Hellmayr and Conover (1949) admitted that they had seen *C. cheriway* only from north of the Amazon River but cited records of that form from Santarem and Rhomes, south of the river. At the same time, they reported that specimens from Marajó and Mexiana Islands, in the mouth of the Amazon, belonged to *C. plancus.* The only actual evidence of intermediacy mentioned by Hellmayr and Conover (1949:283–284) was based on two adult birds from Obidos, Brazil, classified as *C. cheriway,* "which, by more heavily barred lateral upper

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TABLE 1. Plumage characters of *Caracara cheriway* and *C. plancus*.

Character—area	*C. cheriway*	*C. plancus*
1 Breast	dark spots or wedge-shaped bars, heavier posteriorly	dark and light bars over entire breast area
2 Vent area	pale patch between thighs	dark feathers between thighs
3 Upper back/Scapulars	pale wedge-shaped patch with broad black bars, scapulars always black	finely barred, no wedge-shaped patch, scapulars usually heavily barred, only lightly in n. part of range
4 Lower back	black	barring continuous with upper back and tail
5 Upper tail coverts	white or faintly barred	barred

tail coverts, mark a decided step in the direction of *plancus*."

Friedmann and coworkers (1950) and the American Ornithologists' Union (AOU 1957) retained *C. cheriway* as a species. Wetmore (1965) paraphrased Swann (1925) in mentioning intergradation south of the Amazon and accepted "the present-day tendency to unite" the two mainland forms. Brown and Amadon (1968) considered *C. plancus* and *C. cheriway* conspecific as did Blake (1977), who briefly noted "evidence of intergradation in Brazil." Vuilleumier (1970) was the first to treat the insular *C. lutosus* as a well-marked subspecies of the combined *C. plancus,* apparently following the suggestion of Brown and Amadon (1968:736) that if *cheriway* and *plancus* were combined, then "it would be no great extension to include *lutosus*." Stresemann and Amadon (1979) and Sibley and Monroe (1990) merged the continental forms but retained *C. lutosus* as an allospecies. The AOU (1983, 1998) merged all the taxa, noting the report of intergradation "near the mouth of the Amazon." Thus, the merger of *C. plancus* and *C. cheriway* is based mainly on Hellmayr's and Conover's (1949:283) statement that color characters were "merely differences of degree", and on the two specimens of *C. cheriway* from Obidos, Brazil, that they stated showed a "marked step" in the direction of *C. plancus*. The degree of intergradation or variation has never been thoroughly examined in the limited geographical area where the northern and southern populations meet, and the distinctiveness of *C. lutosus* has not been reviewed since Friedmann (1950).

METHODS

To reevaluate the taxonomic relationships of the crested caracaras at the species level, we compared five plumage characters and three body measurements of specimens from all continental geographic populations. All plumage color comparisons were made under museum Examolites® or in daylight. We took measurements on more than 392 specimens of wing chord, bill depth (at the cere), bill length (from the base of the bill to the tip), and tarsus of sexed adult birds from all parts of the species' range. Tarsal measurements were extremely variable within populations and were deemed not useful for comparison. Measurements of males and females were analyzed separately to determine sexual variation.

We used an early version of Table 1 to categorize plumage characters in specimens examined, and we asked colleagues at some other museums (see acknowledgments) to use that and xeroxed photographs of Fig. 1 to evaluate specimens for us, thereby avoiding the need of extensive loans of these large birds. Voice recordings and tissue samples of this species are insufficient for accurate analysis at this time.

Specimens from the northern populations were compared with those from Bolivia and southern Brazil south to Tierra del Fuego. Twenty-one specimens from localities in Brazil along the Amazon River and the northeastern coast of Brazil are from the contact zone of the two populations and were examined separately for plumage patterns. These were compared with northern and southern populations to determine the extent of variation within this region. Because this species is not sexually dichromatic in plumage color or pattern, adult specimens (definitive plumage) were not separated for plumage comparisons.

At the subspecies level we examined the purported characters of recently recognized taxa (Hellmayr and Conover 1949, Peters 1931), all of which were described long ago from the periphery of the range of the species.

South American collecting localities were confirmed using Stevens and Traylor (1983), Paynter (1988), and Paynter and Traylor (1991). Descriptive statistics, AN-

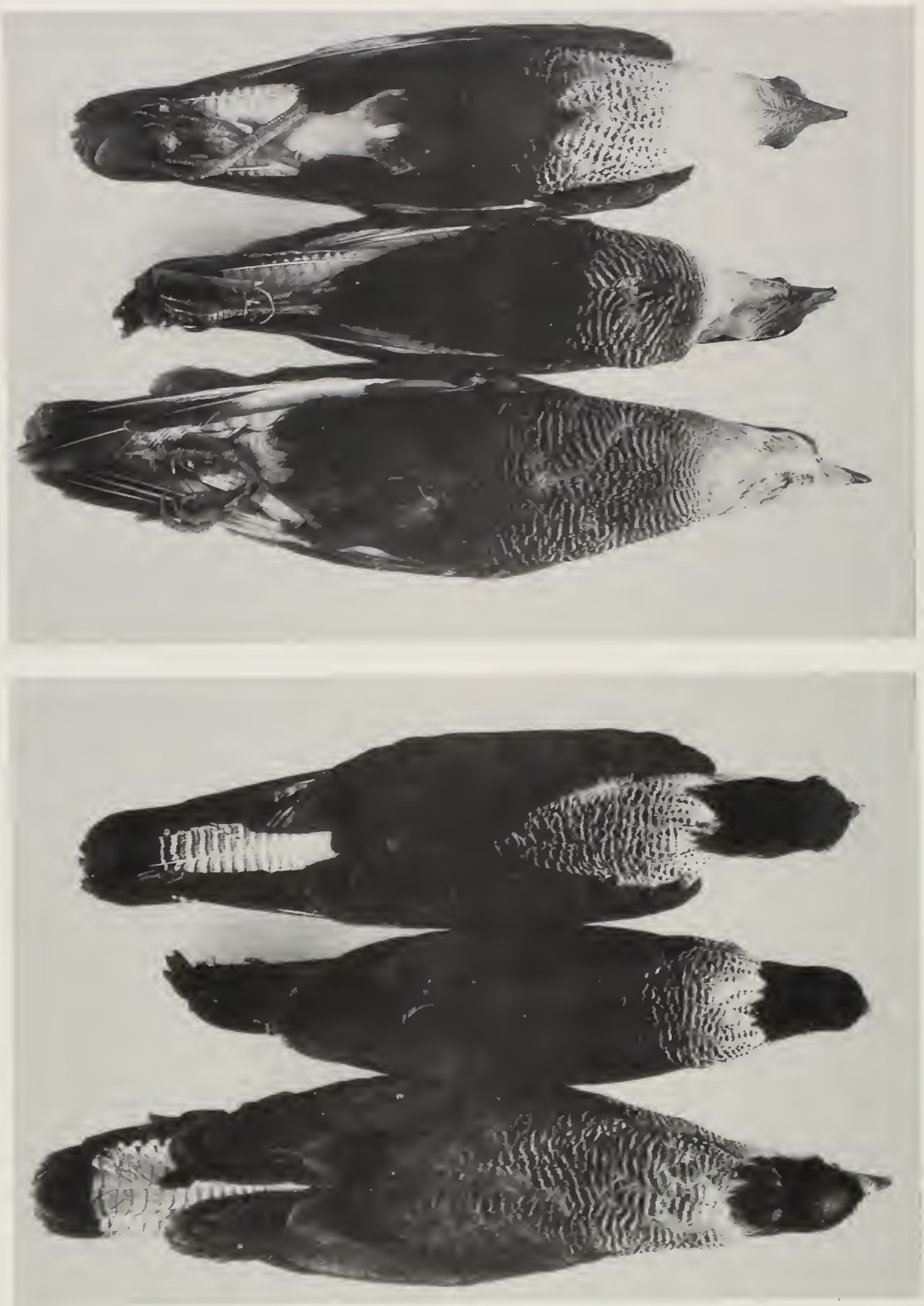

FIG. 1. Typical adult plumage, ventral (above) and dorsal (below) views of (top) *Caracara cheriway* (USNM 132707, Sonora, Mexico), (middle) specimen from zone of contact (USNM 276906, Maica, Brazil), and (bottom), *C. plancus* (USNM 284790, Argentina).

OVAs, and *t*-tests were done with SYSTAT (1992) version 5.0 for Windows.

RESULTS

Specific variation.—Typical adult crested caracaras from south (*C. plancus*) and north (*C. cheriway*) of the Amazon have clearly distinct color patterns (Fig. 1) with major differences in all five plumage characters. The plumage patterns of specimens from the northern and southern portions of the range do not overlap, and specimens from these populations can be identified and allocated unequivocally to either *C. cheriway* or *C. plancus* on that basis. All adult birds from northern Brazil (Roraima), Venezuela, Colombia, Ecuador, and Peru (Rio Chinchipe, Pacasmayo, and Catacaos) north to the United States (except Guadalupe Island) are of the *C. cheriway* type. Birds from southern Brazil (Bahia) and Bolivia to Tierra del Fuego are of the *C. plancus* type. In addition to the plumage differences evaluated (Table 1), the undertail coverts of *C. cheriway* are either all white, or faintly or incompletely barred, giving the base of the tail a whitish appearance, whereas the undertail coverts of *C. plancus* are finely barred with distinct wide white and narrow dark bars that extend completely across the feather. The base of the tail is more white than barred on *C. cheriway* specimens, but this character does not always hold true because some *C. cheriway* specimens have barring near the base of the tail.

Plumage patterns of specimens from the zone of contact.—The apparent zone of secondary contact for the two populations extends from the mouth of the Amazon River westward along the river and its southern tributaries to the Rio Tapajós (Fig. 2). It may extend west as far as the Rio Purus (Canutama), where two immature specimens (Field Museum of Natural History; FMNH 100805, 100806) having mosaic plumage tendencies were collected. A bird from farther west on the Rio Juruá (Museum of Comparative Zoology; MCZ 173161) is pure *C. plancus* and was not considered to represent the contact zone. The zone extends to the southeast from the mouth of the Amazon to approximately Morros de Mariana. The latest specimen collected from the contact zone that we found was dated 1937.

In two adult specimens (American Museum of Natural History; AMNH 241501, 241502) from well to the south at Remanso, on the Rio São Francisco, the plumage on the upper back/scapular area is similar to *C. cheriway,* but the lower back area is intermediate in color between *C. cheriway* and *C. plancus.* The breast of a bird (Naturhistorisches Museum, Vienna; NMWZ 39885) from Juazeiro, Bahia, was scored as *C. cheriway.* Specimens from other nearby Bahia localities (AMNH 163138, Salvador; The Natural History Museum; BMNH 73.3.19.4, Ilha de Itaparica; NMWZ 39884, Lago de Parnagua; NMWZ 39886, Barra) all are pure *C. plancus.* The appearance of these few *cheriway*-like characters well to the south may indicate a much wider zone of intergradation than we recognize, but the lack of available specimens from the intervening 500 km makes this conclusion problematical. This observation may merely be a reflection of the generally more variable plumage in the southern population. Gyldenstolpe (1951) also has commented on the lack of comparative material from parts of the range of this species.

Hellmayr and Conover (1949) mentioned birds from two other localities (Santarem and Rhomes) in the zone and we accepted their determination of those birds as *cheriway* (Table 2). We found no gradual intergradation in plumage characters but instead an abrupt shift in plumage type. There was no consistent pattern of intermediacy but rather a mosaic of plumage combinations. A summary of the plumage data shows that 54% of the 115 individual character states were like *C. plancus,* 40% were like *C. cheriway,* and 6% were intermediate. The lower back (character 4) received 4 of the 6 intermediate ratings. Specimens rated intermediate in this character have dark backs with white-tipped, not barred, feathers in the mid- to lower back region. No specimen was intermediate in more than one character. Seven of the birds from the contact zone were rated as pure for one or the other species.

The two specimens from Obidos that were the basis for the original merger of the species do not agree in plumage patterns. FMNH 101538 is typical *C. cheriway,* whereas FMNH 101539 has the breast and heavily barred tail pattern typical of *C. plancus* and

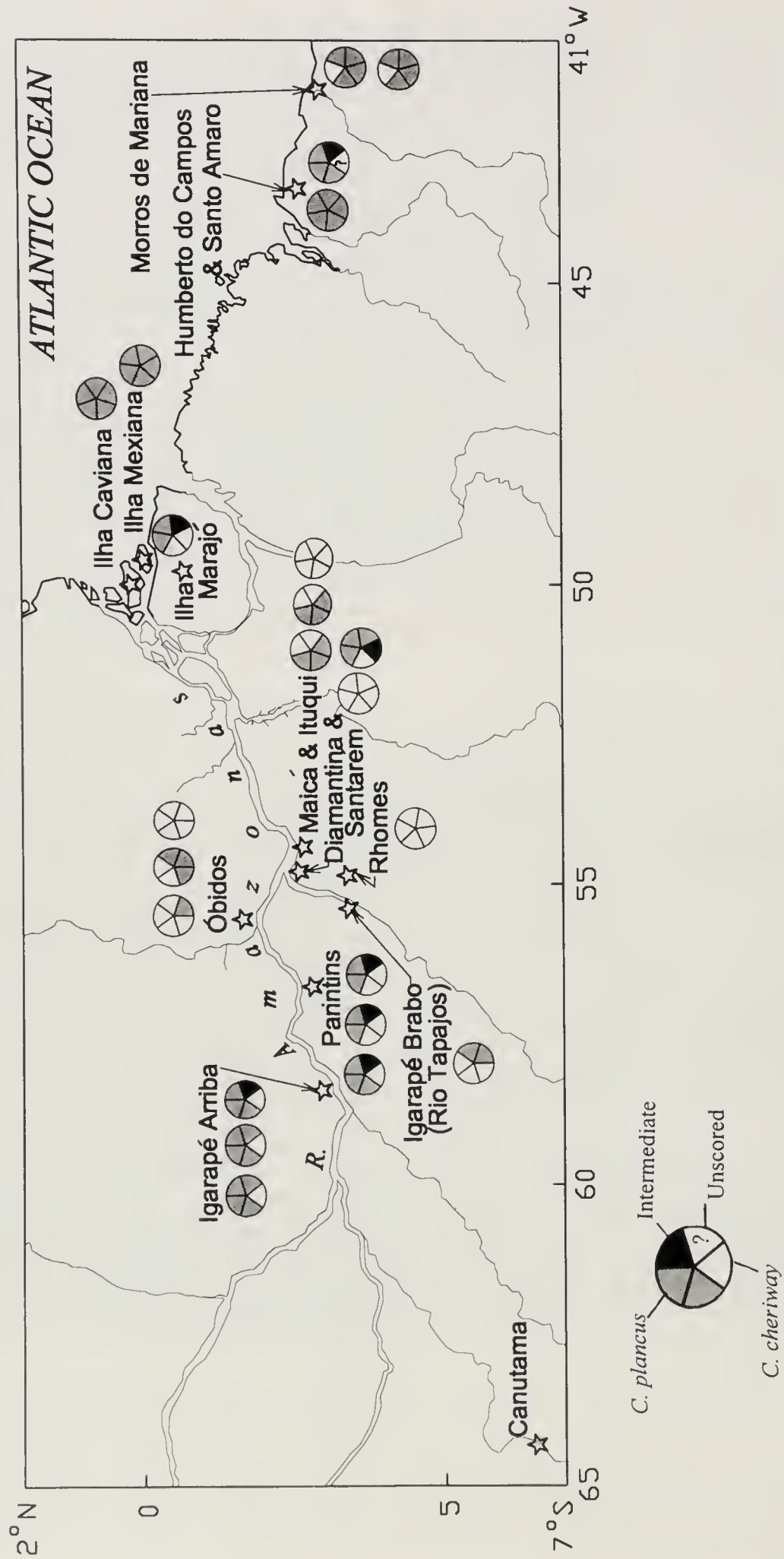

FIG. 2. Map of localities in zone of contact with icons corresponding to character states listed in Table 2.

TABLE 2. Summary of plumage characters (numbers from Table 1) of specimens from the zone of contact between northern and southern continental populations of crested caracaras. Localities without specimen numbers are included on the basis of records mentioned by Hellmayr and Conover (1949). C = *C. cheriway*, P = *C. plancus*, I = intermediate, ? = unscored.

Locality	Museum #	Character				
		1	2	3	4	5
Óbidos	FMNH 101538	C	C	C	C	C
	FMNH 101539	P	P	C	C	P
	BMNH 1908.8.21.17	P	C	C	C	C
Igarpé Arriba	FMNH 101424	P	P	C	P	P
	FMNH 101425	P	P	C	P	P
	FMNH 101427	P	P	C	I	P
Diamantina Parintins	USNM 121077	I	P	C	P	P
	AMNH 276706	P	P	C	I	P
	AMNH 277572	P	C	C	I	P
	AMNH 277573	P	C	C	I	P
Maicá Ituqui	USNM 276906	P	P	C	C	P
	FMNH 101157	C	P	C	P	P
	FMNH 101158	C	C	C	C	C
Agarapé Brabo (Rio Tapajos)	AMNH 285747	P	P	C	C	C
Humberto do Campos (Maranho)	FMNH 100401	P	P	P	P	P
Santo Amaro Maranhao	MCZ 92682	I	?	P	P	P
Morros de Mariana	AMNH 241499	P	C	P	P	P
	AMNH 241500	P	C	P	P	P
Ilha Mexiana	BMNH 73.3.19.4	P	P	P	P	P
Ilha de Marajo	MCZ 22996	P	I	C	C	P
Ilha Caviana	UM 7504	P	P	P	P	P
Santarem		C	C	C	C	C
Rhomes		C	C	C	C	C

the back pattern of *C. cheriway* with the wedge-shaped barring on the upper back and completely black mid- and lower back. An additional specimen from Obidos (BMNH 1908.8.21.17) is typical of *C. cheriway* except for the barring on the breast. Our efforts to locate the two other specimens from Obidos mentioned by Hellmayr and Conover (1949: 284) were unsuccessful.

Size variation.—We divided mensural data from the continental populations into four geographic sets as indicated in Table 3. A one-way analysis of variance shows significant differences among the four continental groups in wing length ($F = 27.8$, $P < 0.01$, $n = 336$), bill length ($F = 3.4$, $P < 0.02$, $n = 376$), and bill depth ($F = 4.2$, $P < 0.007$, $n = 391$), but body size, as estimated by wing chord measurements, was positively correlated with latitude (Fig. 3). Although individual variation in body size is extensive throughout the range, specimens from the extreme southern parts of South America are the largest. Northern and southern populations were analyzed separately for sexual size dimorphism. *t*-tests of northern and southern populations revealed a significant sexual size difference in the northern population, with females being larger (wing length, $t = -5.50$, $n = 243$; bill length, $t = -5.96$, $n = 271$; bill depth, $t = -6.93$, $n = 277$; $P < 0.001$ in all measurements) but no difference in the southern populations (wing length, $t = -1.37$, $n = 77$; bill length, $t = -0.65$, $n = 84$; bill depth, $t = -0.84$, $n = 92$; $P > 0.05$ in all measurements). That the ostensible gap in measurements between *C. cheriway* and extreme southern birds was bridged by specimens from intermediate localities, was used by Hellmayr and Conover (1949) as an argument to justify conspecific treatment. Our data (Table 3, Fig. 3) show that these caracaras vary clinally within each hemisphere, and become smaller toward the equator. This is true for wing chord, bill length, and bill depth.

TABLE 3. Descriptive statistics for four geographic groups of continental crested caracaras and the Guadalupe Island caracara.

		Wing (mm)	Bill length (mm)	Bill depth (mm)
US, Cuba, Mexico	♂ n[a] = 85		90	92
	R[b] = 343–409		28.6–36.7	16.2–19.9
	$\bar{x}$[c] = 382.51		32.65	17.70
	SD[d] = 13.67		1.47	0.75
	♀ n = 79		84	86
	R = 363–415		29.8–38.7	16.5–22.0
	$\bar{x}$ = 391.27		33.60	18.3
	SD = 11.35		1.44	0.88
Central Am. &	♂ n = 42		51	51
Northern South Am.	R = 353–409		29.5–35.0	14.8–19.2
	$\bar{x}$ = 374.17		32.13	17.24
	SD = 12.14		1.27	0.84
	♀ n = 37		46	48
	R = 358–407		31.1–36.4	15.7–20.0
	$\bar{x}$ = 383.57		33.28	18.05
	SD = 11.64		1.31	0.81
Contact Zone	♂ n = 10		13	14
	R = 351–401		30.2–34.7	16.3–18.9
	$\bar{x}$ = 379.5		32.32	17.31
	SD = 16.15		1.41	0.88
	♀ n = 6		8	8
	R = 359–406		29.2–33.8	17.3–18.8
	$\bar{x}$ = 386.00		31.7	18.04
	SD = 16.54		1.55	0.48
Southern South Am.	♂ n = 35		40	43
Incl. S. Brazil	R = 358–438		26.5–37.7	14.9–21.4
	$\bar{x}$ = 397.34		32.49	17.92
	SD = 22.46		2.37	1.47
	♀ n = 42		44	49
	R = 361–455		28.2–37.3	15.7–21.4
	$\bar{x}$ = 404.45		32.82	18.18
	SD = 22.84		2.28	1.44
Guadalupe Island	♂ n = 1			
	406		32.2	17.8
	♀ n = 2			
	401.5		31.0	18.2

[a] n = number of specimens measured.
[b] R = range.
[c] $\bar{x}$ = mean.
[d] SD = standard deviation.

DISCUSSION

Species limits.—We conclude that there are 3 species of crested caracaras: *Caracara plancus, C. cheriway,* and *C. lutosus.* Our examination of nearly 400 specimens from the continental range of the crested caracaras (*Caracara*) revealed a mix in plumage characters of the northern and southern populations only in the limited zone of contact near the Amazon River in Brazil. We consider this limited character sharing a result of secondary contact, first suggested by Vuilleumier (1970). The specimens indicate an abrupt shift in appearance from the northern to the southern plumage pattern, and most of the intermediate specimens exhibit a non-consistent mosaic of characters (back pattern, breast). Juvenile birds from the contact zone exhibit the same tendencies, but were not studied as extensively as adults.

The essential reproductive isolation of these populations is expressed by the low number of intermediate characters in specimens from the contact zone, and the relatively narrow

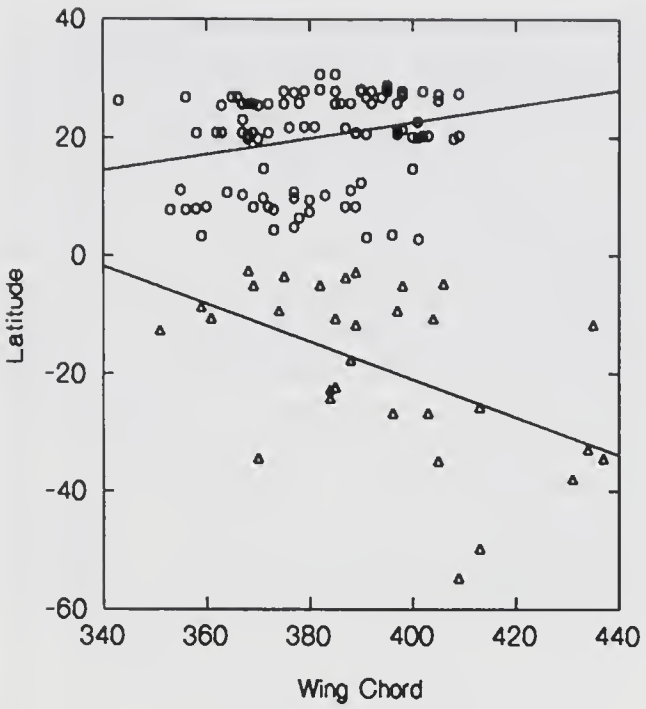

FIG. 3. Linear regression model of size (indicated by wing chord) and latitude of 196 specimen records. Triangles represent specimens from south latitude and circles represent specimens form north latitude.

area of overlap. Crested caracaras are not widespread in Amazonia east of the Andes, occurring only as wanderers in isolated patches of savanna in Amazonian Colombia, Ecuador, and Bolivia. Individuals of the two forms probably meet only infrequently when they wander into areas of sufficiently open habitat along the Amazon River. There is no record of contact of the populations in western South America. Localities of South American specimens reveal a distributional gap from northern Peru (excluding three *cheriway* specimens taken from coastal Peru and the Peru-Ecuador border) south to the middle of Chile. Parker and coworkers (1982) indicate that crested caracaras are uncommon or rare in southern Peru, and Johnson (1965) reports they are very scarce and confined to the sea coast in the two northernmost provinces of Chile (see map 77 in Brown and Amadon 1968).

Review of the Guadalupe Island species.—Morphologically, adults of the extinct Guadalupe Island population differ from those of North and South American mainland populations more than the latter two differ from one another. The crest of *C. lutosus* is brown rather than black, and the crest feathers are longer than those of mainland specimens. The throat is buff to pale brown, not white. Ventral and dorsal surfaces of the rest of the body are entirely banded with brown and white or buff, and there is no solid abdominal patch as in the mainland populations. Remiges and some scapulars are solid brown rather than black; most upper-wing coverts are bordered narrowly with darker brown. Sexed adult representatives of extinct *C. lutosus* are rare in collections, and only three specimens were measured (see Table 3). They do not differ in size from mainland birds.

A few specimens from southern South America (e.g., U.S. National Museum, USNM 13926, Patagonia) show some resemblance to *C. lutosus*. These South American mainland birds are primarily brown rather than black, and most of the body, except for the thighs and a small abdominal patch, is banded. However, the banding is finer on the mainland birds than in *lutosus*. It was undoubtedly birds like this that Ridgway (1876:460) alluded to when he stated "This species resembles the *P. tharus* [= *C. plancus*] much more than *P. cheriway*. . . ." An explanation for the morphological similarity of birds at opposite ends of the range, with birds of quite different appearance occupying the intervening continent, would be speculative at this stage.

We agree with Ridgway (1876) that the Guadalupe Island birds are specifically distinct. Recognition of that distinct and isolated population follows logically from our separation of *C. cheriway* from *C. plancus*, but we suggest that the extinct *C. lutosus* should be recognized at the species level regardless of the treatment of the mainland populations.

Intraspecific variation.—Both southern (*C. plancus*) and northern (*C. cheriway*) crested caracaras have been variously divided at the subspecific level by different authors. Populations of the Southern Caracara (*C. plancus*) from northern Paraguay to the Amazon have frequently been separated under the trinomial *C. p. brasiliensis* (Gmelin, 1788) on the basis of being darker and smaller (Swann 1925, Wetmore 1926, Peters 1931). The name *brasiliensis* cannot be applied to any caracara (Banks and Dove 1992), and Gyldenstolpe (1951) has indicated that the subspecific name *caracara* Spix, 1824 must be used if two forms of birds south of the Amazon are recognized. However, we are unable to document

any consistent difference in plumage pattern, color, or size among these birds, and so we follow most recent authors (Hellmayr and Conover 1949, Gyldenstolpe 1951, Blake 1977, Stresemann and Amadon 1979) in recognizing the populations south of the Amazon as being monotypic *Caracara plancus.*

Populations of the northern mainland species, *C. cheriway,* have been recognized by up to four subspecific names (*cheriway* Jacquin, 1784; *audubonii* Cassin, 1865; *pallidus* Nelson, 1898; *ammophilus* van Rossem, 1939). Divisions in this species have been based on the amount and intensity of black as opposed to brown on the wings and back, and on size. The amount of black is subject to individual variation, and depends on stage of molt and extensive fading related to the open habitat occupied by the species. Contrary to Griscom (1932), we do not believe that fading from black to brown occurs post mortem. Size varies less than some earlier writers have suggested and increases clinally from the Amazon to the north (Fig. 3), so that the birds in the southern United States tend to be among the largest. There are no major changes in these characters to warrant the recognition of van Rossem's (1939) *ammophilus* of Sonora, Mexico with a supposedly smaller bill and feet and more prominently barred tail, or, despite the present disjunction of range, the trinomial *audubonii* that Cassin (1865) based on Florida's larger birds. We agree with Stresemann and Amadon (1979) in considering those names synonyms of *C. cheriway.*

Nelson (1898) separated birds from the Tres Marias Islands off western Mexico under the subspecific name *pallidus,* on the basis of paler or lighter brown coloration and slightly smaller size. Grant (1965) agreed that the island birds are generally paler brown than those on the mainland but attributed the difference to greater fading of the island birds. We agree that the color is not diagnostic, and note that new feathers or those generally hidden from solar radiation are no paler on the island birds than on those from elsewhere in the range. Furthermore, AMNH 471349, taken by Nelson at the Tres Marias, is dark both dorsally and ventrally. Grant (1965) considered a shorter terminal tail band and a shorter wing and tarsus in males to be sufficient for recognition of *pallidus,* even though comparable differences could not be demonstrated in females. However, tarsus length is too individually variable to be a useful taxonomic character. Wing and culmen lengths given by Nelson (1898) and Grant (1965) fit well in the range of variation of the much larger mainland sample we measured (Table 3). We believe that the minor difference in the length of the terminal tail band may be related to wear of the rectrices and that other differences of tail band characters mentioned by Grant (1965) are not sufficient to warrant separation of the Tres Marias population. Some specimens from the Tres Marias exhibit extensive barring on the abdomen, but this is within the range of variation of the mainland specimens. Thus, we synonymize *pallidus* with *C. cheriway.*

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VISUAL COMMUNICATION AND SEXUAL SELECTION IN A NOCTURNAL BIRD SPECIES, *CAPRIMULGUS RUFICOLLIS*, A BALANCE BETWEEN CRYPSIS AND CONSPICUOUSNESS

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ABSTRACT.—Cryptic protective mechanisms and the conspicuousness required to communicate result in a conflict of opposing selection. In the Red-necked Nightjar (*Caprimulgus ruficollis*) a nocturnal bird, the use of a restricted signaling strategy provides an appropriate balance between these two selection forces. Conspicuous white wing and tail bands may have been favored by sexual selection in this species. We studied the variation of visual signals and found conspicuousness to be closely related to sex and age, being much higher in males and adults. This variation allows an individual to identify the reproductive status of conspecifics, providing sexual selection a basis to select these visual signals in this and other nocturnal bird species. We believe that a relationship between restricted signaling strategy and sexually selected visual signals may occur in nocturnal species that use visual comunication. *Received 24 April 1998, accepted 5 Feb. 1999.*

Crypsis is one of the more effective antipredator mechanisms (Baker and Parker 1979). Because it relies on inconspicuousness, its use can conflict with the conspicuousness required for communication. Selection pressure drives populations to address signals among conspecifics (conspicuousness increases at close range) and to conceal them from predators (inconspicuouness or long range crypsis; Butcher and Rohwer 1989). An appropriate balance between crypsis and communication is achieved by the use of restricted signaling, for example, the presence of hidden conspicuous signals in highly specific body zones that are only exhibited in some situations (see Butcher and Rohwer 1989).

In strictly nocturnal birds, which account for less than 3% of all bird species (Martin 1990), the visual channel is assumed to play an insignificant role in communication compared to diurnal birds. However, this is only an assumption and nocturnal birds may use visual signals to communicate more widely than is thought. The Red-necked Nightjar (*Caprimulgus ruficollis*) is a nightbird of open and semi-open habitats that uses sight to capture flying insects. The plumage of caprimulgids is highly cryptic, but includes white spots on wings, tail, and throat. These markings, because of their anatomical location, are only visible in some contexts (agonistic, antipredator, and sexual displays) when the sender intentionally shows its markings to the receiver (Bent 1940, Mengel 1972, Bruce 1973, Cramp 1985, Fry et al. 1988, Cleere 1998, Aragonés et al. in press). Some caprimulgid species have been reported to show individual variation in spot size and color (Common Nighthawk, *Chordeiles minor*, Selander 1954; Red-necked Nightjar, Beven 1973, Soares 1973; Blackish Nightjar, *C. nigrescens*, Ingels and Ribot 1982). This variation in spots suggests that signal conspicuousness might vary with age and sex.

The objective of this paper is to describe the variation of spots in signal conspicuousness in the Red-necked Nightjar and to examine whether this variation is related to age and/or sex. We hypothesize that if males, especially adult males, show greater conspicuousness in wing and tail bands, then these plumage characters may be sexually selected.

METHODS

We used data from 170 specimens obtained from bird collections at Estación Biológica de Doñana, CSIC (n = 22) and from road casualties (n = 148) in Córdoba (southern Spain) during the 1986 to 1994 breeding seasons. From this sample we measured the following variables related to conspicuousness. (1) Band size. The wing-band consisted of 3 to 4 spots and the tail-band of 2 to 3 spots. Using a digital caliper, the longer and shorter axis of each spot was measured (± 0.1 mm) and the area for each was calculated. The surface areas of the spots present in the outer primaries of the right wing were summed and recorded as wing-band size and those on right rectrices were summed and recorded as tail-band size. The area of each spot

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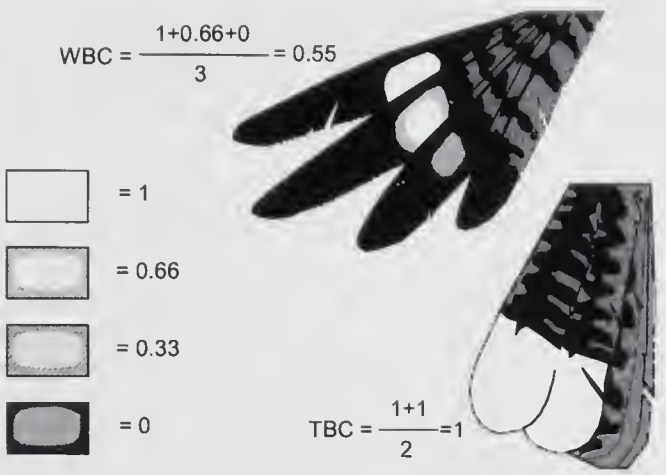

FIG. 1. Wing-band (WBC) and tail-band contrast (TBC), calculated from color and sharpness values of spots forming the bands (1 = maximum contrast value, white spot with sharp contrasting edges, 0 = minimum contrast value, dark spots without sharp contrasting edges).

was indexed by the product of the long and the short axis. (2) Band contrast. Contrast was measured from the color and sharpness of the spots that formed the wing and tail bands. The contrast gradient was established from a reference series formed by four types of spots that were assigned the values 0, 0.33, 0.66 and 1; where 0 denoted the spot with the darkest colour and least sharp contrasted edges, and 1 that with the lightest color and sharpest edges. A given individual can possess spots of different types (depending on color and sharpness variations), so each spot was assigned a value, and a mean index was used for the contrast analysis in wing-band contrast and tail-band contrast which included all spots of the wing and tail (Fig. 1). (3) Uniformity of color spots within a band. Some individuals showed bands consisting of a single type of spot, whereas others had one or two different types; the former were designated "uniform" and the latter "non-uniform". (4) Spot number in wing and tail bands. (5) Band conspicuousness. Band size and contrast values were first log transformed, normalizing the data for the application of parametric statistics and used to calculate a conspicuousness index (C) from the following expression:

$$C = WBS \times \log(WBC+1) + TBS \times \log(TBC+1)/WBS + TBS$$

where WBS = wing-band size, TBS = tail-band size, WBC = wing-band contrast, and TBC = tail-band contrast. This index varied from 0 to 1, with 1 corresponding to maximum conspicuousness. Sex was determined by gonadal dissection. Differences in band size and conspicuouness were analysed by ANOVA and the Tukey test, and differences in the number of spots and their uniformity by means of the G-test. Contrast differences were identified by multiple logistic regression, which allows one or more categorical variables (contrast in our case) to be analysed and related to a dependent variable. This method is especially suitable for data that are not normally distributed and is more effective than other classifying methods such as discriminant analysis (Press and Wilson 1978; see also Harrell 1986, Schlinger 1990, Fancy et al. 1993). Conspicuousness data were transformed logarithmically for parametric analysis. All analyses were performed using JMP software (version 2, Macintosh computer).

RESULTS

There were significant differences in wing-band size ($F = 31.47$, df = 3, 90, $P < 0.001$) and tail-band size ($F = 41.61$, df = 3, 90, $P < 0.001$) between sex–age categories. Wing and tail bands were significantly larger in males than in females and larger in adults relative to young. There was a clear trend for band size to increase in an age-sex sequence, both in wing-band (mean young females = 662.3 ± 37.87 SD, $n = 29$; mean adult females = 803.1 ± 52.66, $n = 15$; mean young males = 986.3 ± 37.24, $n = 30$; mean adult males = 1210.5 ± 45.61, $n = 20$) and in tail band (mean young females = 743.4 ± 67.06, $n = 29$; mean adult females = 1046.4 ± 93.24, $n = 15$; mean young males = 1428.7 ± 65.93, $n = 30$; mean adult males = 1852.6 ± 80.75, $n = 20$). Both variables were found to be positively correlated ($r = 0.67$, $n = 93$, $P < 0.001$).

The multiple logistic regression discriminated between the four age-sex classes in terms of wing-band or tail-band contrast (Table 1). There were significant differences in sex and age for wing-band contrast ($\chi^2_3 = 86.33$, $P < 0.001$, $n = 94$) and tail-band contrast $\chi^2_3 = 94.21$, $P < 0.001$, $n = 94$). Males and adults always had the largest contrast index both for wing-band and tail-band (Fig. 2). Sharp edges were detected only in males with wing-band or tail-band contrast index close to one because only such spots had sharp edge contrasts. Males showed greater uniformity in wing-band contrast than females, and adults were more uniform than young in this respect. All groups showed uniform tail bands (Table 2).

The presence of four spots on the wing is an exclusive feature of adult males (Table 2); over 45% ($n = 16$) of adult males have the fourth spot. About 80% of adult males also tended to possess three caudal spots ($n = 28$; Table 2). Additional spots on the tail was not significantly different among the other groups (Table 2). The additional wing spot increased

TABLE 1. Parameter estimates of logistic functions derived from multiple logistic regression.

Logistic function parameters	Estimate	Wald test	*P*
(Young female vs adult female)			
Intercept 1	9.47	17.62	<0.001
Wing-band contrast	−13.22	21.22	<0.001
(Adult female vs young male)			
Intercept 2	7.52	11.51	<0.001
Wing-band contrast	−10.17	14.43	<0.001
(Young male vs adult male)			
Intercept 3	1.63	0.56	>0.05
Wing-band contrast	−1.34	0.32	>0.05
(Young female vs adult female)			
Intercept 1	10.05	23.21	<0.001
Tail-band contrast	−16.03	31.09	<0.001
(Adult female vs young female)			
Intercept 2	8.45	16.36	<0.001
Tail-band contrast	−12.29	20.59	<0.001
(Young male vs adult male)			
Intercept 3	6.09	10.54	<0.001
Tail-band contrast	−6.90	10.20	<0.001

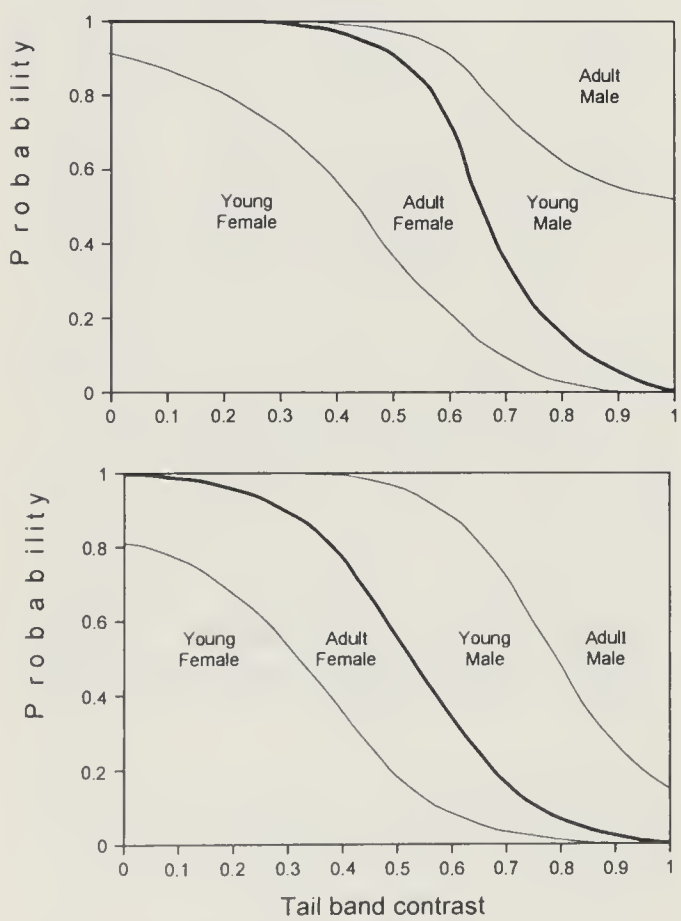

FIG. 2. Heavy line indicates probability of belonging to a sex class as a function of wing-band contrast (WBC) or tail-band contrast (TBC), thin lines indicates probability of belonging to an age class.

the wing-band size of adult males an average of 6% and the tail-band size of adult males an average of 12%. The presence of additional spots on wing and tail increased the overall band area by 9.6% and presumably increased signal conspicuousness. There were significant differences in conspicuousness (Table 2) with regard to age–sex classes, with greater conspicuousness in males and adults.

DISCUSSION

We detected a marked trend for signal conspicuousness to increase with age and in males which was reflected in an increase of contrast, number of spots, wing- and tail-bands area, and uniformity of contrast. The differences in conspicuousness in wing- and tail-bands were related to the age and sex class of the individual. Potentially, these signals let conspecifics evaluate one another in aggressive or reproductive contexts. Signal conspicuousness seemingly involves little energy expenditure but is combined with expensive displays; the combination results in an efficient signal that conveys a much greater amount of information (Hasson 1991). We found that spot number was related to sex and age, but Forero and coworkers (1995) found no statistically significant differences in the average

TABLE 2. Frequency distribution of contrast uniformity, additional spots in bands and conspicuousness index for age-sex groups.

	Female		Male		
	Young	Adult	Young	Adult	*P*
Contrast uniformity (n = 94)	n = 29	n = 15	n = 30	n = 20	
WBC[a] (G_3 = 27.29)	37%	66%	66%	95%	<0.001
TBC[a] (G_3 = 11.09)	88%	87%	91%	89%	>0.05
Additional spots (n = 170)	n = 50	n = 31	n = 54	n = 35	
In wing (G_3 = 40.33)	0%	0%	0%	55%	<0.001
In tail (G_3 = 39.85)	6%	6%	6%	80%	<0.001
Conspicuousness (n = 94)	n = 29	n = 15	n = 30	n = 20	
(F = 71.76, n = 3, 90)	0.23	0.43	0.43	0.91	<0.001

[a] WBC = wing-band contrast, TBC = tail-band contrast.

number of spots between groups of the same species. We believe the addition of new spots has a strong biological significance because it occurs only in adult males as reported by Forero and coworkers (1995), but their method, failed to demonstrate a significant difference.

In the Red-necked Nightjar increased signal conspicuousness may increase the likelihood of mating (Andersson 1982, Andersson 1992, Saetre et al. 1994), and conspicuous males may have a higher mating success (Payne 1982, Price 1984, Järvi et al. 1987, Harvey

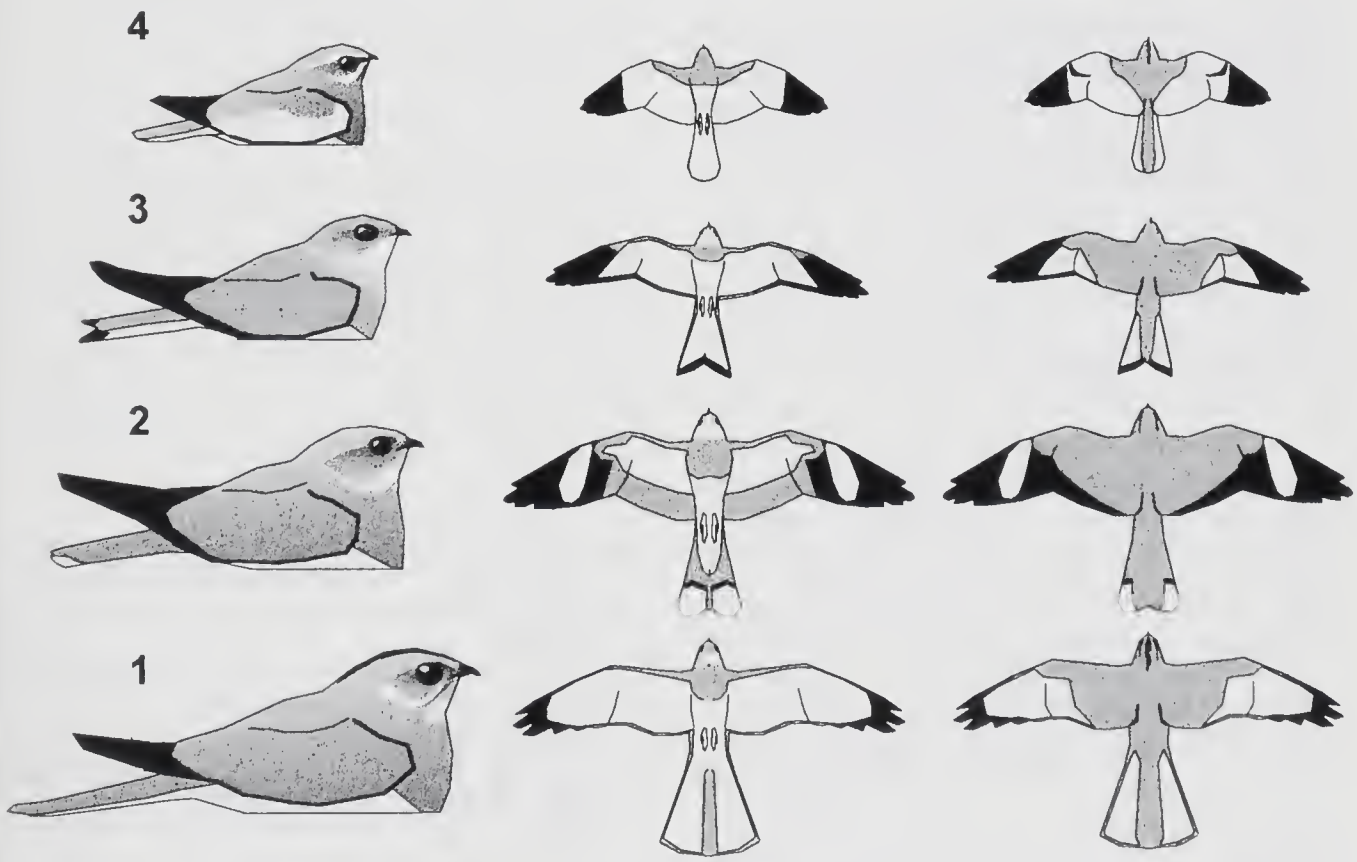

FIG. 3. For restricted signaling strategy to be effective, conspicuous plumage zones (black and white areas in the drawing) must be concealed by eryptic plumage zones (gray areas in the drawing) while at rest. A hypothetical model based on the genus *Caprimulgus* (1) represents the maximum possible conspicuousness for restricted signaling strategy; a larger conspicuous area would defeat the defensive system based on erypsis and hence caneel restrieted signaling strategy. The Nacunda Nighthawk (2), the Sand-Colored Nighthawk (3) and the White-Winged Nigthjar (4) use three restricted signaling strategies that are very similar to that of the model, esspecially the Sand-Colored Nighthawk.

and Bradbury 1991, Sundberg and Larsson 1994). The fact that increased signal conspicuousness was associated with adult males suggests that the signal could be modified by sexual selection (Höglund 1993). For adult males, this signal indicates that those individuals have survived at least two reproductive seasons and, therefore, may reflect a high reproductive quality. In another nocturnal bird species, the Great Snipe (*Gallinago media*) males have white spots on their tails, and females choose the males with the whitest signals (Höglund et al. 1992). This suggests that signal conspicuousness in nocturnal birds could be an effective way of distinguishing between potential mates.

Our results show that in Red-necked Nightjar both sexes possess ornaments, and that in both sexes spots tend to increase in conspicuousness with age. Forero and coworkers (1995) claimed that visual signals increased only in males. We believe that their results are due to a less precise method of measuring spot size.

The restricted signaling strategy allows two scarcely compatible mechanisms to be combined and might occur in many cryptic species of the genera *Burhinus, Charadrius* and *Gallinago,* although this has not yet been investigated. For a nocturnal signal, contrast is more important than color, as in the caprimulgids and other species that use restricted signaling strategy with white spots (i.e., *Gallinago media,* Höglund et al. 1992; *Burhinus* spp., Martin 1990, Hayman et al. 1986). Therefore, increasing the amount of white color increases contrast and presumably maximizes the signaling ability. Similar trends of increasing conspicuousness with age have been detected in other caprimulgids (Little Nightjar, *C. parvulus heterurus,* Schwartz 1968; Chuck-Will's-Widow, *C. vociferus,* Rohwer 1971; Blackish Nightjar, Ingels and Ribot 1982; Scrub Nightjar, *C. anthonyi,* Robbins and Ridgeley 1994; Nacunda Nighthawk, *Podager nacunda,* Aragonés unpubl. data; Pauraque, *Nyctidromus albicollis,* Aragonés 1997a, b).

From the distribution of visual signals in Red-necked Nightjar (throat, wings, and tail-bands), we developed a model plumage pattern for a nightjar that represents the optimum/maximum distribution of conspicuous areas in the body (Fig. 3). We subsequently found that the Nacunda Nighthawk and the White-Winged Nightjar (*Caprimulgus candicans*) have patterns that closely resemble our model, and the Sand-colored Nighthawk's (*Chordeiles rupestris*) visual signals patterns are identical with that of the model. All three are gregarious South American species of open or semiopen habitats with sexual variations in wing- and tail-bands (Ffrench 1986, Hilty and Brown 1986, Sick 1993). It is interesting to note that the Sand-colored Nighthawk and the Yellow-billed Tern (*Sterna superciliaris*), two Amazonic species that use the same fluvial habitat, show almost identical visual signal patterns and general appearance (see Sick 1993). This convergent evolution stresses the significance of open and semiopen habitats for restricted signaling strategy evolution. Such habitats are also characterized by other species that employ this strategy, *Burhinus* spp. and the Great Snipe (Hayman et al. 1986). We believe that a relationship between restricted signaling strategy and sexually selected visual signals may occur in nocturnal species that uses visual comunication.

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INTERSPECIFIC INTERACTIONS WITH FORAGING RED-COCKADED WOODPECKERS IN SOUTH-CENTRAL FLORIDA

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ABSTRACT.—Interspecific competition for Red-cockaded Woodpecker (*Picoides borealis*) cavities has been well documented and may be one factor contributing to the species' decline. Other forms of interspecific interactions have rarely been documented over most of the species' range and have received little attention. During 806 hours of Red-cockaded Woodpecker foraging observations in south-central Florida we documented 306 interspecific interactions with 19 species. We observed fewer non-foraging interactions (98) than foraging interactions (208). Red-cockaded Woodpeckers lost 70 (71%) of the non-foraging interactions and 177 (85%) of the foraging interactions. Most non-foraging interactions (64%) were with non-woodpecker species, several of which frequently and consistently dominated Red-cockaded Woodpeckers. Together, Eastern Kingbirds (*Tyrannus tyrannus*), Great Crested Flycatchers (*Myiarchus crinitus*), Eastern Bluebirds (*Sialia sialis*), and Pine Warblers (*Dendroica pinus*) won 45 of their 48 (94%) non-foraging interactions with Red-cockaded Woodpeckers. Most foraging interactions (97%) were with other woodpecker species. Red-bellied Woodpeckers (*Melanerpes carolinus*) were involved in 172 (85%) of these interactions, of which they won 168 (98%). We found no relationship between the rate of interactions and the habitats or the local landscape in which these interactions occurred. Red-cockaded Woodpeckers did not appear to move to different and possibly less productive foraging sites after being usurped. In south-central Florida, where hardwood basal areas are relatively low in Red-cockaded Woodpecker habitat, the foraging niche of these two species may overlap to a greater extent than elsewhere in their range. *Received 20 July 1998, accepted 5 Feb. 1999.*

The Red-cockaded Woodpecker (*Picoides borealis*) is a cooperative breeder restricted to the old growth pine forests of the southeastern United States (Jackson 1971). Despite nearly 30 years of Federal protection, Red-cockaded Woodpecker populations have continued to decline (James 1991). Habitat loss and fragmentation have ultimately been responsible for the species' decline (Lennartz et al. 1983, Conner and Rudolph 1991). Interspecific competition for Red-cockaded Woodpecker nest and roost cavities has been well documented (Jackson 1978, Harlow and Lennartz 1983, Kappes and Harris 1995) and may be one proximate factor contributing to the species' decline (U.S. Fish and Wildlife Service 1985).

Interspecific interactions, other than those involving cavities, have rarely been reported over most of the Red-cockaded Woodpecker's range (Morse 1970, Nesbitt et al. 1978). Hooper and Lennartz (1981) observed foraging Red-cockaded Woodpeckers from May to March in South Carolina and documented 21 interspecific interactions between Red-cockaded Woodpeckers and one of four woodpecker species or the Brown-headed Nuthatch (*Sitta pusilla*). Only three interactions were related to foraging. Ligon (1970) reported six interactions between Red-cockaded Woodpeckers and Downy (*Picoides pubescens*) and Hairy woodpeckers (*P. villosus*) during 240 hours of observations from May to December in north-central Florida. In contrast, Nesbitt and coworkers (1981) documented 149 interspecific interactions between Red-cockaded Woodpeckers and five woodpecker species during 221 hours of observations from July to October in southwestern Florida. Most interactions involved Red-bellied Woodpeckers (*Melanerpes carolinus*) that often usurped Red-cockaded Woodpeckers from foraging sites. These interactions may have reduced the caloric intake of foraging Red-cockaded Woodpeckers (Nesbitt et al. 1981).

Geographic variation in interactions between species is common (Travis 1996). Explaining this variation may lead to a better understanding of geographical differences in be-

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havior, demography, and habitat selection of potentially interacting species. In this paper we report on interspecific interactions with Red-cockaded Woodpeckers in a small population in south-central Florida.

METHODS

The Avon Park Air Force Range (AFR) is a 42,900 ha, multiple-use, active military training installation in Polk and Highlands counties, Florida. Dominant native pine communities consist of longleaf (*Pinus palustris*) and south Florida slash pine (*P. elliottii* var. *densa*) and approximately 9,000 ha planted in north Florida slash pine (*P. elliottii* var. *elliottii*). The pine habitats are interspersed with other communities typical of this region such as oak scrub and fresh water marshes. The natural pine habitats support the characteristic bird community for this region (Engstrom 1993), including 21 groups of Red-cockaded Woodpeckers.

To determine the foraging preferences of Red-cockaded Woodpeckers at Avon Park AFR, we observed individuals from 12 groups once a month from April 1995 to March 1996. Red-cockaded Woodpeckers were observed from dawn to dusk whenever possible; observations that ended prior to 13:00 EST were repeated. During a foraging observation period, we recorded the location of the focal individual, its foraging maneuver, and substrate use at 10 minute intervals. Locations were entered into a Geographical Information System (ArcView GIS Version 3.0). We determined home range boundaries and overlaid these boundaries with existing habitat type coverages. From these maps, we calculated the area of each habitat type (13 categories) in each home range and linked individual foraging locations to specific habitat types. These habitat types included pine flatwoods, scrubby flatwoods, oak scrub, sand pine scrub, pine plantation, mixed natural pine and plantation, pine swamp, oak hammock, hardwood forests, cypress, marsh, lake, and human disturbed.

During a subset (806 hours) of the total observation time (1168 hours), we documented all interspecific interactions. We recorded the species, sex (if determinable), type of aggression (aerial chase, tree chase, lunge, usurp, etc.), and the outcome (winner/loser). Individuals that retreated without retaliation were classified as losing. We categorized interactions as foraging or non-foraging interactions. Interactions where the winner examined, or foraged at, the usurped site were categorized as foraging related. All other interactions were categorized as non-foraging. Monthly observation periods varied as did the number of individuals in each group. To avoid observation time and group size biases, we used only those interactions that involved the breeding pair in each cluster and converted those interactions to a rate per hour for all analyses. We used the number of interactions between all individuals to describe the species involved in interspecific interactions with Red-cockaded Woodpeckers, and the number, type and outcome of those interactions.

Because most interactions were instantaneous or no longer than 15–60 s (aerial chases), we assumed interactions between the same individuals were independent if they occurred more than 15 min apart. For interactions that occurred less than 15 min apart, we excluded all but the first interaction as long as the type of interaction (foraging or non-foraging) and habitat were the same. When the type of interaction or habitat differed, we excluded all the interactions, since they could not be aggregated into a single type of interaction. However, if we suspected two different individuals of the other species (e.g., one male and one female) were involved in sequential interactions less than 15 min apart then both observations were considered independent.

To examine whether the frequency of interspecific interactions was habitat specific, we compared the frequency of interactions per habitat type to the expected frequency based on the proportion of time Red-cockaded Woodpeckers foraged in each habitat type. To determine if the frequency of interspecific interactions was related to the local landscape, we compared the frequency of interactions per group to the mean basal area of pines and hardwoods in each Red-cockaded Woodpecker's home range. Given the frequency of foraging interactions between Red-cockaded and Red-bellied woodpeckers, we repeated the above analyses for those interactions.

To determine whether usurpations had a measurable effect on Red-cockaded Woodpecker foraging patterns we performed two analyses. First, we compared the habitats used by Red-cockaded Woodpeckers before and after interactions with Red-bellied Woodpeckers to determine whether the former moved to a different and potentially less productive habitat after an interaction. Second, we compared foraging tree characteristics [dbh (diameter at breast height) and height] and Red-cockaded Woodpecker foraging height before and after usurpations by Red-bellied Woodpeckers to determine whether they moved to different micro-sites after interactions. Male and female Red-cockaded Woodpeckers forage at different locations (Ligon 1970), therefore we analyzed each sex separately. All statistical tests were nonparametric and were performed in the Microsoft Windows 95 operating system using SPSS (version 8.0).

RESULTS

We observed 306 independent interspecific interactions between 45 color-banded Red-cockaded Woodpeckers and 19 other bird species (Table 1). Interactions involved 26 breeding adult Red-cockaded Woodpeckers (13 ♂, 13 ♀), 10 hatch-year birds (6 ♂, 4 ♀), 6 older helpers (all ♂), and 2 floaters (both ♂). Of the 306 interactions observed, 203 occurred with the breeding Red-cockaded Woodpeckers, 50 with hatch-year birds, 16 with older helpers, and 6 with floaters. Red-cockaded Woodpeck-

TABLE 1. Species observed interacting with Red-cockaded Woodpeckers, the outcome (loser or winner), and the type (foraging or non-foraging) of interaction during 806 hours of foraging observations at the Avon Park Air Force Range, 1995–1996.

Species	Red-cockaded Woodpecker Loser		Red-cockaded Woodpecker Winner	
	Foraging	Non-foraging	Foraging	Non-foraging
Red-shouldered Hawk	—	1	—	1
Red-bellied Woodpecker	168	6	4	8
Red-headed Woodpecker	—	3	—	—
Northern Flicker	1	—	1	2
Yellow-bellied Sapsucker	—	—	—	2
Downy Woodpecker	2	—	23	11
Hairy Woodpecker	3	—	—	3
Eastern Kingbird	1	14	—	—
Great Crested Flycatcher	—	11	—	—
Florida Scrub-Jay	—	1	—	—
Blue Jay	2	—	—	—
Brown-headed Nuthatch	—	1	1	—
Eastern Bluebird	—	8	—	1
Loggerhead Shrike	—	3	—	—
Northern Mockingbird	—	3	—	—
Pine Warbler	—	12	2	—
Eastern Towhee	—	2	—	—
Red-winged Blackbird	—	4	—	—
Summer Tanager	—	1	—	—
Total # of Interactions	177	70	31	28
Total # of Species	6	14	5	7

ers lost 247 (81%) interactions to 18 species and won 59 (19%) interactions with 9 species (Table 1). Win:loss ratios for Red-cockaded Woodpeckers did not differ between life history stage ($\chi^2 = 1.23$, df = 3, $P > 0.05$) or sex ($\chi^2 = 1.49$, df = 1, $P > 0.05$).

Interactions between Red-cockaded Woodpeckers and other woodpecker species were most frequent, accounting for 237 (77%) of all interactions. Excluding species with fewer than five observed interactions, five species won more than 85% of their interactions with Red-cockaded Woodpeckers [Eastern Kingbird (*Tyrannus tyrannus*), 100%; Great Crested Flycatcher (*Myiarchus crinitus*), 100%; Red-bellied Woodpecker, 94%; Eastern Bluebird (*Sialia sialis*), 89%; and Pine Warbler (*Dendroica pinus*), 86%; Table 1]. The Downy Woodpecker was the only species Red-cockaded Woodpeckers consistently dominated (34 of 36 encounters).

The rate of interspecific interactions with breeding Red-cockaded Woodpeckers was greatest in June and July. Although interactions varied between months from 0.10 (± 0.03 SE) to 0.40 (± 0.31) interactions per hour (Fig. 1a), these differences were not significant (Kruskal-Wallis One Way ANOVA: $\chi^2 = 16.7$, df = 11, $P > 0.05$).

Non-foraging interactions.—Red-cockaded Woodpeckers had 98 non-foraging interactions with 18 species; however, they had only non-foraging interactions with 12 of those species (Table 1). Interactions with Red-headed Woodpeckers (*Melanerpes erythocephalus*), Eastern Kingbirds, Great Crested Flycatchers, Northern Mockingbirds (*Mimus polyglottos*), and Pine Warblers often involved aerial chases that lasted from 15–60 s. Few of these interactions were initiated by Red-cockaded Woodpeckers. However, in one instance a group of Red-cockaded Woodpeckers mobbed and successfully evicted a Red-shouldered Hawk (*Buteo lineatus*). Of the 98 interactions, Red-cockaded Woodpeckers won 28 and lost 70.

Non-foraging interactions were most frequent during June and July (Fig. 1b) and monthly differences were statistically different (Kruskal-Wallis One Way ANOVA: $\chi^2 = 23.9$, df = 11, $P = 0.013$).

Foraging interactions.—Red-cockaded

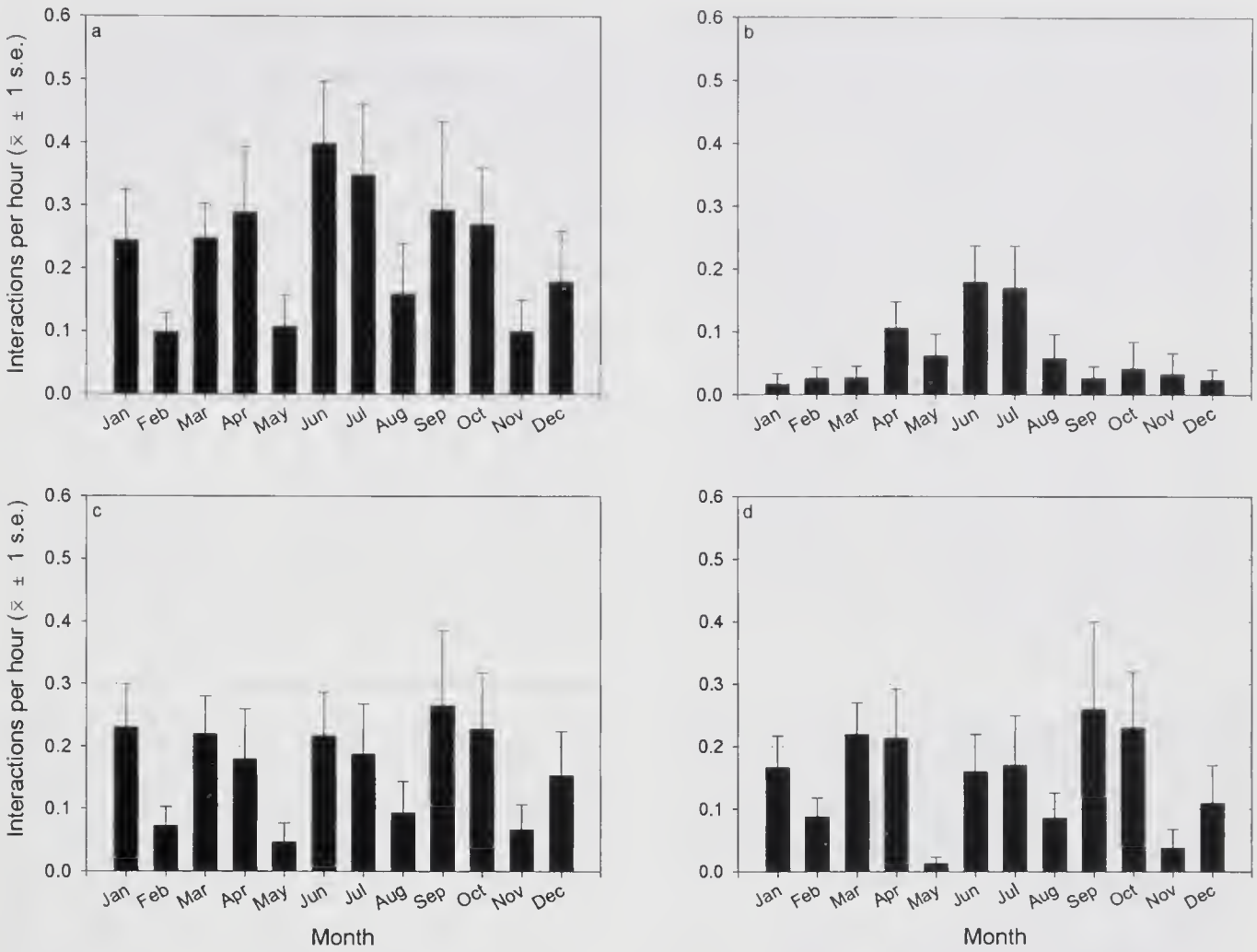

FIG. 1. Interspecific interactions ($\bar{x}$ ± 1 SE for each month) observed per hour with breeding adult Red-cockaded Woodpeckers at Avon Park Air Force Range, in south-central Florida, 1995–1996: (a) all interactions, (b) non-foraging interactions, (c) foraging interactions, and (d) all interactions with Red-bellied Woodpeckers.

Woodpeckers had 208 foraging interactions with eight species. With six of these species they had both foraging and non-foraging interactions, but foraging interactions were more frequent than non-foraging interactions (Table 1). Most foraging interactions were between Red-cockaded Woodpeckers and other woodpeckers (202 of 208, 97%), but interactions with Blue Jays (*Cyanocitta cristata*), Eastern Kingbirds, Brown-headed Nuthatches, and Pine Warblers also were observed. Red-cockaded Woodpeckers lost most (177 of 208, 85.1%) foraging interactions; however, 74% of the 31 interactions they won were with Downy Woodpeckers. Red-cockaded Woodpeckers lost a greater percentage of foraging interactions (85.1%) than they did non-foraging interactions (71.4%; $\chi^2 = 7.14$, df = 1, $P = 0.008$). None of the foraging interactions were initiated by Red-cockaded Woodpeckers, except for those with Downy Woodpeckers. Downy Woodpeckers frequently foraged near Red-cockaded Woodpeckers and often were aggressively chased and their foraging locations usurped. The rate of foraging interactions with breeding Red-cockaded Woodpeckers did not vary monthly (Kruskal-Wallis One Way ANOVA: $\chi^2 = 14.2$, df = 11, $P = 0.22$; Fig. 1c).

Red-bellied Woodpeckers.—Most interspecific interactions occurred between Red-cockaded and Red-bellied woodpeckers (186 of 306, 61%). Of the 186 interactions between Red-cockaded and Red-bellied woodpeckers, the latter won 174 (94%). Red-bellied Woodpeckers successfully usurped foraging Red-cockaded Woodpeckers in all but 4 of 168 foraging interactions. Red-bellied Woodpeckers frequently foraged within sight of Red-cockaded Woodpeckers but usurped them only after the Red-cockaded Woodpecker had found food. We also observed Red-bellied Wood-

TABLE 2. Variation in habitat characteristics and the rate ($\bar{x} \pm 1$ SE) of all interspecific interactions (per hour of observation), foraging and non-foraging interactions, and interactions with Red-bellied Woodpeckers, with breeding Red-cockaded Woodpeckers from different groups at the Avon Park Air Force Range, 1995–1996.

RCW group	Pine basal area (m^2/ha)	Hardwood basal area (m^2/ha)	All interactions	Foraging interactions	Non-foraging interactions	Red-bellied Woodpecker interactions
1	8.13	0.0	0.16 ± 0.09	0.11 ± 0.07	0.05 ± 0.04	0.10 ± 0.06
2	12.44	0.0	0.19 ± 0.05	0.15 ± 0.05	0.04 ± 0.04	0.11 ± 0.04
3	8.97	0.0	0.20 ± 0.06	0.17 ± 0.01	0.04 ± 0.02	0.14 ± 0.06
5	6.6	0.28	0.20 ± 0.06	0.15 ± 0.01	0.06 ± 0.03	0.14 ± 0.06
7	7.49	0.07	0.10 ± 0.05	0.06 ± 0.03	0.04 ± 0.04	0.04 ± 0.02
8	9.28	0.04	0.10 ± 0.06	0.04 ± 0.02	0.06 ± 0.06	0.04 ± 0.02
15	11.34	0.03	0.42 ± 0.09	0.27 ± 0.09	0.15 ± 0.05	0.22 ± 0.09
19	9.18	0.46	0.22 ± 0.07	0.18 ± 0.07	0.04 ± 0.02	0.15 ± 0.05
21	10.25	0.44	0.17 ± 0.11	0.11 ± 0.07	0.05 ± 0.04	0.11 ± 0.07
23	6.55	0.01	0.42 ± 0.15	0.34 ± 0.13	0.08 ± 0.03	0.35 ± 0.14
31	12.15	0.86	0.22 ± 0.09	0.16 ± 0.08	0.07 ± 0.03	0.13 ± 0.07
33	12.33	0.0	0.34 ± 0.09	0.24 ± 0.07	0.09 ± 0.04	0.22 ± 0.02

peckers following Red-cockaded Woodpeckers as they foraged between different pine stands. Red-cockaded Woodpeckers won only 12 interactions with Red-bellied Woodpeckers: 4 foraging interactions and 10 non-foraging interactions.

The rate of interactions between Red-bellied Woodpeckers and breeding Red-cockaded Woodpeckers varied monthly (Kruskal-Wallis One Way ANOVA: $\chi^2 = 19.3$, df = 11, $P = 0.055$; Fig. 1d); however, no consistent pattern was evident. The rate of interactions did not differ between the breeding and non-breeding season (Mann-Whitney *U*-test: Z = -0.59, $P > 0.05$). No sex-related difference existed in the rate of interactions between Red-cockaded and Red-bellied woodpeckers ($\chi^2 = 5.13$, df = 1, $P > 0.05$).

Habitat relationships.—Red-cockaded Woodpeckers foraged predominately (93.8% of observation time) in pine flatwood, scrubby flatwood, and pine plantation habitats (Bowman et al. 1998, unpubl. data). The frequency of foraging and non-foraging interactions did not differ from the relative frequency of habitats used by foraging Red-cockaded Woodpeckers ($\chi^2 = 4.74$ and 2.18, df = 4 and 2, respectively, $P > 0.05$). We also found no significant correlations between the rate of interactions and the area of any of the 13 habitat types in Red-cockaded Woodpecker home ranges (Pearson correlations: all $P > 0.05$). Pine basal area in home ranges varied from 6.6 to 12.4 m^2 per ha, and hardwood basal area varied from 0.0 to 0.44 m^2 per ha (Table 2); however, neither the total number of interactions nor foraging or non-foraging interactions were correlated with the basal area of pines or hardwoods within each home range.

Interactions with Red-bellied Woodpeckers in different habitat types did not differ from the relative frequency of habitats used by Red-cockaded Woodpeckers ($\chi^2 = 0.18$, df = 3, $P > 0.05$). However, the rate of these interactions was positively correlated with the percentage of each home range comprised of pine plantation (Spearman rank correlation: $r = 0.62$, $P < 0.05$). No significant correlations existed between the rate of interactions and the area of any of the other 12 habitat types or the pine or hardwood basal area in Red-cockaded Woodpecker home ranges (Spearman rank correlation: all $P > 0.05$).

Red-cockaded Woodpeckers moved to a new habitat type following only 5 of 120 (4%) usurpations by Red-bellied Woodpeckers for which we had data. No significant difference existed in the dbh or height of the trees used by foraging Red-cockaded Woodpeckers (male or female) before and after usurpation (Kruskal-Wallis One Way ANOVAs: all $P > 0.05$), nor did any differences exist in the height at which Red-cockaded Woodpeckers (male or female) foraged before and after usurpation (Kruskal-Wallis One Way ANOVAs: all $P > 0.05$).

DISCUSSION

Thirty-two percent of interspecific interactions were not related to foraging. Non-foraging interactions were highly seasonal, occurring during the breeding season for most species. Many of these interactions may have been related to nest and/or fledgling defense as many occurred near nests or young of the species interacting with Red-cockaded Woodpeckers. Although these interactions were seasonal and relatively infrequent in our population, other forms of non-foraging interactions (e.g., cavity competition) could play an important role in the dynamics of Red-cockaded Woodpecker populations (Kappes and Harris 1995).

Most interspecific interactions were related to foraging and occurred between Red-cockaded and Red-bellied woodpeckers. Red-cockaded Woodpeckers lost virtually all foraging interactions with Red-bellied Woodpeckers. Red-cockaded Woodpeckers interacted frequently with Downy Woodpeckers, winning most encounters. Therefore, the latter interactions likely had no deleterious impacts on Red-cockaded Woodpeckers.

Habitat use, foraging behavior, and diet of Red-cockaded and Red-bellied woodpeckers appear to be dissimilar. Red-bellied Woodpeckers use most habitats occurring within their range (Sprunt 1954, Breitwisch 1977 and references within) but may prefer hardwood habitats (Short 1982, Root 1988). In Florida, their use of tree species for foraging is diverse and varies by habitat type (Breitwisch 1977). Red-bellied Woodpeckers spend 20–69% of their foraging time on dead trees (Williams 1975, Breitwisch 1977, Williams and Batzli 1979). In contrast, Red-cockaded Woodpeckers forage almost exclusively on living pines (Hooper and Lennartz 1981) in relatively open pine forests.

In south Florida pine habitat, Breitwisch (1977) observed foraging Red-bellied Woodpeckers gleaning and probing (80%) but rarely excavating (10%). At Avon Park AFR, foraging Red-cockaded Woodpeckers used surface probes (54%) most frequently, excavated frequently (40%), and rarely gleaned (4%; Bowman et al.1998, unpubl. data).

Little dietary overlap appears to exist between Red-cockaded and Red-bellied woodpeckers (Beal 1911). Red-bellied Woodpecker stomachs (n = 271) contained 31% animal matter, of which 6% was ants; Red-cockaded Woodpecker stomachs (n = 76) contained 81% animal matter, of which 56% was ants. Both species consumed a similar percentage of beetles (~10%); however, little overlap existed in the remaining fraction of animal matter.

Niche overlap between these two species appears to be low, even in south Florida, yet interactions between Red-bellied and Red-cockaded woodpeckers appear to be higher here than elsewhere in their ranges. It is possible that these interactions are simply overlooked elsewhere, especially if they are more frequent outside of the breeding season. If so, and these interactions have deleterious impacts on Red-cockaded Woodpeckers, then they should be examined more closely elsewhere. However, geographical variation in interspecific competition may be real and be caused by variation in population densities of the species (Thompson 1988), indirect effects as species assemblages change, the productivity or vegetation composition of habitats (Travis 1996) or some interaction of these factors.

Data on the density of Red-bellied Woodpeckers across their range are not available; in general they appear as abundant in Florida as elsewhere in the southeastern coastal plain (Bock and Lepthien 1975, Root 1988, Price et al. 1995). At Avon Park AFR, the density of Red-cockaded Woodpeckers is low compared to populations outside of peninsular Florida (Bowman et al. 1998, unpubl. data). Data on the regional variation in density of both Red-cockaded and Red-bellied woodpeckers are needed to determine whether differences in density contribute to variations in interspecific interactions.

Indirect effects related to the presence of other species may have contributed to the high rate of observed interactions. At Avon Park AFR, five species of woodpeckers and the Brown-headed Nuthatch are sympatric with Red-cockaded Woodpeckers; however, many of these species are sympatric in pine habitats outside of peninsular Florida. The abundance and diversity of species utilizing similar resources in different habitats may contribute to

variation in the rate of interspecific interactions.

Differences in pine forests between south-central Florida and more temperate forests may have contributed to the relatively high rates of interactions with Red-bellied Woodpeckers. In southern Florida, most Red-cockaded Woodpeckers occur in mesic and hydric flatwoods. These habitats have lower hardwood basal area than do more temperate pine communities (Beever and Dryden 1992, pers. obs.). Elsewhere, Red-bellied Woodpeckers' preference for hardwoods may minimize their foraging overlap with Red-cockaded Woodpeckers, but we know little about habitat-specific foraging strategies of either species. Although hardwood basal area varied among the 12 Red-cockaded Woodpecker home ranges, overall, basal area was low and was not correlated with the frequency of Red-bellied Woodpecker interactions.

All Red-cockaded Woodpecker populations in peninsular Florida support fewer than 50 groups (Cox et al. 1995). In peninsular Florida, Red-cockaded Woodpeckers have larger home ranges (Nesbitt et al. 1981; DeLotelle et al. 1983; Bowman et al. 1998, unpubl. data) and produce fewer fledglings (Jansen and Patterson 1983; DeLotelle and Epting 1992; Bowman et al. 1998, unpubl. data) than other populations. These characteristics suggest that these populations may occupy relatively poor quality habitat; however, few correlations exist between various measures of Red-cockaded Woodpecker demography and habitat characteristics (Beyer et al. 1996; Bowman et al. 1998, unpubl. data). Although these results do not suggest a deleterious effect of interspecific competition, the relatively high rates we documented bear further investigation, especially where these interactions have not been reported. Aggressive interaction between species is not sufficient to demonstrate competition, but interspecific competition may contribute to variation in the abundance and reproductive potential of species. It is possible that some synergistic interaction of habitat and community structure, such as competition, may be related to regional differences in Red-cockaded Woodpecker demography.

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SPATIAL AND TEMPORAL DYNAMICS OF A PURPLE MARTIN PRE-MIGRATORY ROOST

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ABSTRACT.—We used simultaneous WSR-88D radar (NEXRAD) and direct visual observations to investigate the spatial and temporal dynamics of a Purple Martin (*Progne subis*) pre-migratory roost in South Carolina. The timing of mass flights of martins from and to the roost was related to levels of ambient light. Each morning, the birds first departed approximately 40 min before sunrise independent of date, with peak departures occurring about 10 min before sunrise. The time of evening flights was more variable, but peak movement of birds into the roost consistently occurred at sunset. Purple Martins exited the roost in organized, annular departures (360°) that were visible on radar up to 100 km away from the roost, but returned to the roost over an extended period in scattered flocks. During morning departures we recorded flight speeds up to 13.4 m/s. Radar echoes corresponding to martin flights were recorded farther from the roost, and flights from and to the roost occurred later and earlier, respectively, in response to increased cloud cover. The departures of birds from the roost appeared to be displaced by winds aloft. At the peak of the roosting season in late July, the total roost population was estimated to be at least 700,000 birds. *Received 18 Aug. 1998, accepted 5 Feb. 1999.*

Purple Martins (*Progne subis*) are neotropical migratory swallows that breed across North America (Brown 1997, AOU 1998). In eastern North America, Purple Martins are conspicuous colonial nesters that almost exclusively are dependent on man-made nesting houses. As a result, martin breeding biology and behavior have been the focus of considerable study (see Brown 1997). After the fledging period eastern populations of Purple Martins often congregate in distinctive nocturnal roosts that may reach concentrations of 100,000 or more as a prelude to fall migration (Brown 1997). From late June through August or early September these assemblages engage in two mass movements daily: a morning exodus from the roost for aerial foraging and an evening return (Allen and Nice 1952). Although the existence of these large pre-migratory roosts is well documented (e.g., Bent 1942, Allen and Nice 1952, Anderson 1965, Brown and Wolfe 1978, Rogillio 1989, Russell et al. 1998), little quantitative data are available concerning their spatial and temporal dynamics.

Studies of communal roosts may be limited by the inability to collect data at appropriate spatial and temporal scales (Caccamise et al. 1983, Russell et al. 1998). Locating roosts often is labor-intensive (see Caccamise and Fischl 1985, Komar 1997). Even when roost locations are known, visual surveys alone provide only limited data on the spatial extent and direction of roosting flights (Brown and Wolfe 1978), and the time of movements (e.g., pre-dawn flights) may limit visual observations (Russell and Gauthreaux 1998). Recently, we developed methods for using the National Weather Service's new doppler weather surveillance radar, the WSR-88D or NEXRAD to locate and study communal roosting assemblages (Russell and Gauthreaux 1998, Russell et al. 1998). In this study, we provide quantitative data on the spatial and temporal dynamics of a pre-migratory roost of Purple Martins in South Carolina using simultaneous WSR-88D radar and direct visual observations. Our specific objectives were to document the daily timing and spatial pattern of roosting flights, flight directions and speeds, the influence of weather conditions on roosting flights, and seasonal changes in roost population size.

METHODS

Study area.—Our study site was a Purple Martin roost on Lunch Island (34° 03′ N, 81° 18′ W), a 5-ha island located in Lake Murray, near Columbia, South Carolina (Russell and Gauthreaux 1998: fig. 2). We conducted visual surveys from a peninsula on the shoreline of the lake, approximately 3 km south of the roost. Radar data were collected at the National Weather Service Office, Columbia Metropolitan Airport, 28 km southeast of the roost site. A detailed description

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of the study area is provided in Russell (1996) and Russell and Gauthreaux (1998).

Survey methods.—We conducted timed visual surveys of roosting flights 5 days per week from 30 June to 27 August 1995. We originally conducted morning surveys from 05:50 to 06:50 EST, but extended them to 07:30 when the duration of departures lengthened in late July. Evening surveys were conducted from 19:15 to 21:15 throughout the study. During each visual survey, we recorded the numbers and flight directions of individual martins as they passed over a natural circular opening (24 m diameter; 48° angle of observation) in the forest canopy, using methods described by Lowery and Newman (1963) and applied to WSR-88D radar by Russell and Gauthreaux (1998). We identified martins in flight by their distinctive profile, behavior, and vocalizations (Brown 1997). The presence of other roosting species was negligible during the study (Russell 1996). When both numbers and flight directions could not be accurately recorded, we (1) assigned directions to flocks, or (2) only made counts for many of the birds. During surveys we also made incidental observations of the roost site with a 30× spotting scope and recorded general weather conditions. We later obtained detailed local climatological data (LCD) from the National Weather Service Office at the Columbia Metropolitan Airport.

Immediately after each visual survey we visited the National Weather Service Office and acquired WSR-88D radar images that coincided with our surveys, except for eight mornings when weather conditions obscured martin flights on radar. Evening flights of Purple Martins typically failed to produce recognizable patterns on the WSR-88D (Russell and Gauthreaux 1998); thus we present no radar data on evening arrivals. We collected base reflectivity images to monitor flights of martins in the proximity of the roost and composite reflectivity images to track flights over a wider geographic area (Russell and Gauthreaux 1998). We also collected several radial velocity images to determine directions and speeds of each mass flight. We recorded radar images by taking a 35-mm color slide exposure of each image as it was displayed on a monitor at the radar site. Detailed descriptions of the WSR-88D, radar images, and our survey methods are provided in Russell and Gauthreaux (1998).

Analyses.—We examined the timing of roosting flights by recording the beginning, end, duration, and peak of each mass flight from both the radar and visual data (Russell and Gauthreaux 1998). We also examined temporal changes in the numbers of departing and arriving birds by pooling our visual counts into 15-min totals based on our timed surveys (Russell 1996). We characterized the spatial patterns of roosting flights by examining the origin, timing, intensity, number, and spatial distribution of echoes from each radar image of the roost area (Russell and Gauthreaux 1998). We measured the maximum spatial extent of each mass flight by relating echoes created from the leading edge of the flight to landmarks depicted on the radar (e.g., county boundaries). We excluded mornings when regional precipitation or spurious ground echoes obscured the maximum extent of flights.

We pooled visual flight tracks of individual birds so that peak movement from or to the roost was not divided artificially (Russell 1996); then examined temporal changes in flight directions using circular statistics (Zar 1984). We scored directions and speeds of each mass flight directly from the radar images (Russell and Gauthreaux 1998).

We used univariate correlation and stepwise multiple regression to examine the influence of weather conditions on roosting flights. Daily climatological data (mean, 04:00, 07:00, 19:00) included temperature, dew point, total precipitation, atmospheric pressure, surface wind speed, visibility, and cloud cover. Variables initially entered or left the stepwise models at $P = 0.1$. We examined the influence of winds aloft on morning departures by scoring the modal azimuth of annular displacement (relative to the roost site; Eastwood et al. 1962) and regressing these values against the corresponding direction of geostrophic winds aloft (1000 m above the ground or 900 mb; Riehl 1972) at 07:00.

The total roost population (TRP) represents the estimated daily sum of all birds at the roost (Caccamise et al. 1983). Based on a preliminary examination of the radar data, we assumed that departures and arrivals of Purple Martins were omnidirectional at approximately equal densities. Our visual sample area was 0.47° or 1/766 of the circumference around the roost at a distance of 3 km. Thus, we calculated separate morning and evening TRPs by multiplying the total count for each movement by 766 (Russell 1996) and examined changes in roost size. We used univariate correlation to investigate relationships between our morning and evening counts, and patterns of flight with time and date. We used JMP 3.1 (SAS Institute 1995) on an IBM computer for all analyses with probability values $P < 0.05$ recognized as significant and means reported ± 1 standard deviation (SD) unless otherwise noted. We standardized all survey times by converting to minutes before or after sunrise or sunset (as given by the National Weather Service Office in Columbia, South Carolina).

RESULTS

Timing of flights.—We detected the initiation of mass departures as a single radar echo corresponding to the location of the roost. Time of initial departure from the roost averaged 41.4 ± 4.0 (SD) min before sunrise (range 31–48 min) and was independent of date ($r^2 = 0.02$, $P > 0.05$, $n = 32$; Russell and Gauthreaux 1998). Time of peak departure also was independent of date ($r^2 = 0.06$, $P > 0.05$, $n = 32$). Mean duration of morning departures (interval from first radar echo to last bird observed visually) was 67.9 ± 12.2 min (range 49–101 min) and was positively

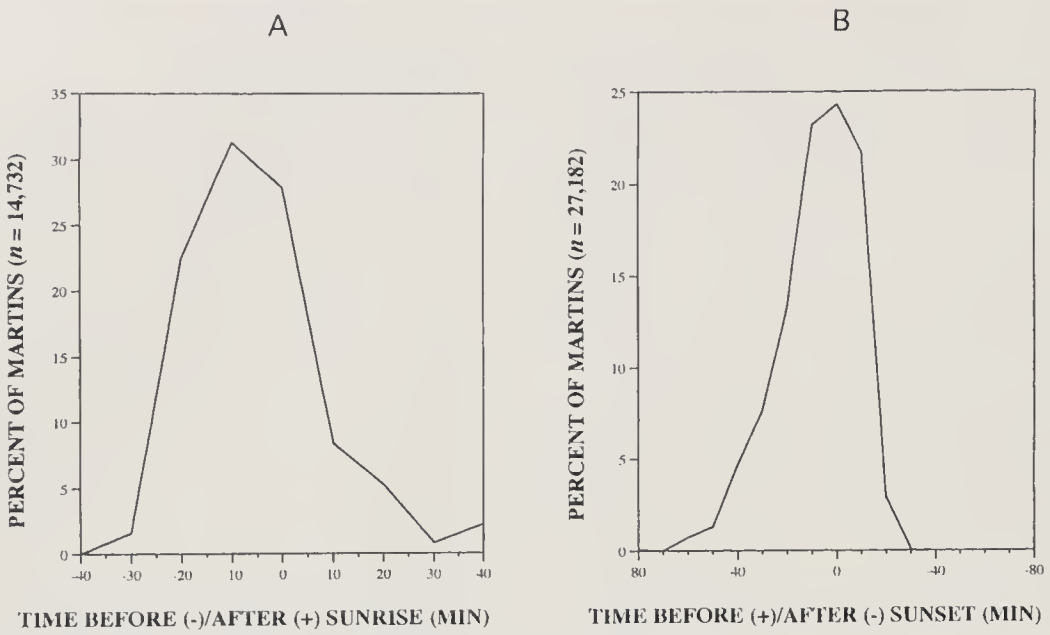

FIG 1. Changing numbers of roosting Purple Martins during visual counts of (A) morning departures and (B) evening arrivals, by time before and after sunrise or sunset.

related to the number of birds counted exiting the roost ($r^2 = 0.60$, $P < 0.001$, $n = 32$).

Changes in the numbers of Purple Martins observed departing the roost were related to the time of sunrise. Because some birds first departed in darkness, changes in the percentage of birds we observed 40–30 min before sunrise reflected their increased visibility in the morning sky rather than actual numbers aloft (Fig. 1A). Corresponding radar data indicated that, on average, the movement of most birds from the roost began 20.4 ± 4.6 min before sunrise, when sufficient light was available for accurate visual counts (Russell and Gauthreaux 1998). The number of birds departing from the roost consistently peaked about 10 min before sunrise, then steadily declined over the next 40 min (Fig. 1A). We occasionally observed a small, secondary increase in the number of birds departing from the roost as late as 30–40 min after sunrise (Fig. 1A).

Purple Martins first returned to the roost an average of 59.8 ± 13.5 min before sunset (range 35–84 min), and the last birds entered the roost 2–24 min after sunset ($\bar{x} = 15.5 \pm 5.9$ min). We found a weak negative relationship between the time that the last birds were observed entering the roost and date ($r^2 = 0.23$, $P = 0.0033$, $n = 36$), but not for the time of peak movement into the roost ($r^2 = 0.07$, $P > 0.05$, $n = 36$). Mean duration of observed evening arrivals at the roost (71.4 ± 15.2 min, range 43–103 min) was not related to our visual counts ($r^2 = 0.05$, $P > 0.05$, $n = 36$), but we detected a negative relationship between the duration of evening flights and date ($r^2 = 0.71$, $P < 0.001$, $n = 36$).

Numbers of Purple Martins returning to the roost increased 50–30 min before sunset (Fig. 1B). At about 30 min before sunset, the number of arrivals increased rapidly until peaking at sunset (Fig. 1B). After sunset, numbers aloft declined rapidly and ceased by 24 min after sunset, and always before complete darkness.

Spatial pattern of flights.—Each morning until the peak of the roosting season, Purple Martins departed en masse from the roost in all directions (360°). These omnidirectional departures first were visible on radar as a roughly circular mass of echoes that extended across Lake Murray (Russell and Gauthreaux 1998: fig. 3). As departures continued, an expanding ring or annulus was seen on radar as the departing birds extended across the landscape directly away from the roost (Russell and Gauthreaux 1998: fig. 4). The maximum daily extent of flights we could detect on radar averaged 77.9 ± 14.1 km (range 50–100 km, $n = 20$; Russell and Gauthreaux 1998). We found no relationship between the maximum distance of flights and date ($r^2 = 0.02$, $P > 0.05$, $n = 20$) or our morning counts ($r^2 = 0.01$, $P > 0.05$, $n = 20$). Beginning 12 August we observed on radar that more birds departed

south than other directions; by 18 August birds only departed to the south and after 26 August we no longer observed departures on radar.

In the evening, Purple Martins arrived at the roost in sporadic, loosely organized flocks. The birds flew over the observation point at tree-top height (ca 18–25 m) and then flew down to just above the lake's surface, usually below the radar beam (Russell and Gauthreaux 1998). After reaching the roost the birds remained aloft in a growing mass that circled high over the island counter-clockwise until a final, spiraling entry into the roost at sunset.

Flight directions and speeds.—During morning departures, the Purple Martins we observed visually were consistently and significantly ($P < 0.001$) oriented to the south. The mean direction (± 95% confidence interval, vector length, angular deviation) of martins at 40–21 min before sunrise was 180° (2°, 0.953, 18°); at 20–1 min before sunrise was 184° (3°, 0.922, 23°); at 0–20 min after sunrise was 183° (4°, 0.884, 28°); at 21–40 min after sunrise was 182° (4°, 0.885, 28°); and at 41–60 min after sunrise was 190° (3°, 0.931, 21°). The radar images also showed the birds flying in a southerly direction over the observation point, consistent with an omnidirectional departure from the roost. Radar images of velocity that we acquired on 32 mornings showed that flight speeds of the departing birds ranged from 10.8–13.4 m/s (see figure 5 in Russell and Gauthreaux 1998).

We observed distinct changes in the orientation of Purple Martins during evening flights to the roost. The mean direction of martins at 90–71 min before sunset was 141° (90°, 0.364, 65°) and not significant ($P > 0.05$). During this time we often observed birds feeding in small flocks and flying away from the roost. As the time of sunset approached, however, the mean direction of martins at the observation point became significant ($P < 0.001$) and increasingly oriented towards the northeast, but still east of the roost (azimuth = 10° from observation point). The mean direction of martins at 70–51 min before sunset was 93° (18°, 0.318, 67°); at 50–31 min before sunset was 73° (14°, 0.399, 63°); at 30–11 min before sunset was 57° (9°, 0.590, 52°); at 10 min before to 9 min after sunset was 54° (5°, 0.836, 33°); and at 10–29 min after sunset was 53° (4°, 0.843, 32°).

Weather conditions and roosting flights.—Purple Martins first departed the roost earlier relative to sunrise with higher atmospheric pressure, surface wind speed, and relative humidity, but later relative to sunrise with increased cloud cover (stepwise multiple regression: $R^2 = 0.66$, $P < 0.001$, $n = 32$). Of these variables, atmospheric pressure was the most important and the only significant univariate relationship ($r^2 = 0.20$, $P = 0.0068$, $n = 32$). We also found a significant relationship between the duration of morning departures and atmospheric pressure (stepwise multiple regression: $R^2 = 0.29$, $P < 0.001$, $n = 32$).

Purple Martins were detected on radar farther from the roost on days with increased cloud cover or decreased visibility at 07:00 (stepwise multiple regression: $R^2 = 0.61$, $P < 0.001$, $n = 20$), although univariate analysis indicated a significant relationship only for cloud cover ($r^2 = 0.35$, $P = 0.0063$, $n = 20$). Mass departures from the roost also appeared to be displaced by winds aloft. Azimuthal wind direction was strongly related to the modal direction of annulus displacement ($r^2 = 0.76$, $P < 0.001$, $n = 20$).

Arrival of the first birds over the observation point was not related to any of the weather variables, but arrival of the last martins at the roost occurred earlier relative to sunset on days with more cloud cover and later in the season (stepwise multiple regression: $R^2 = 0.40$, $P < 0.001$, $n = 36$). Univariate analysis also indicated a significant relationship for cloud cover: ($r^2 = 0.13$, $P = 0.0275$, $n = 36$). Maximum temperature, atmospheric pressure, and surface wind speed at 19:00 were identified by stepwise regression as significant predictors of the duration of evening flights ($R^2 = 0.89$, $P < 0.001$, $n = 36$), although no variable was significant when subjected to univariate analysis.

Seasonal changes in total roost population.—Despite fluctuations in the daily number of departing ($\bar{x} = 368.3 \pm 201.9$ SD, range 29–916, $n = 14{,}732$ birds) and returning ($\bar{x} = 755.1 \pm 548.9$ SD, range 108–2,531, $n = 27{,}182$ birds) martins, the roosting population exhibited a seasonal pattern of growth and decline (Fig. 2). On the first morning census of 3 July we counted only 172 birds over the ob-

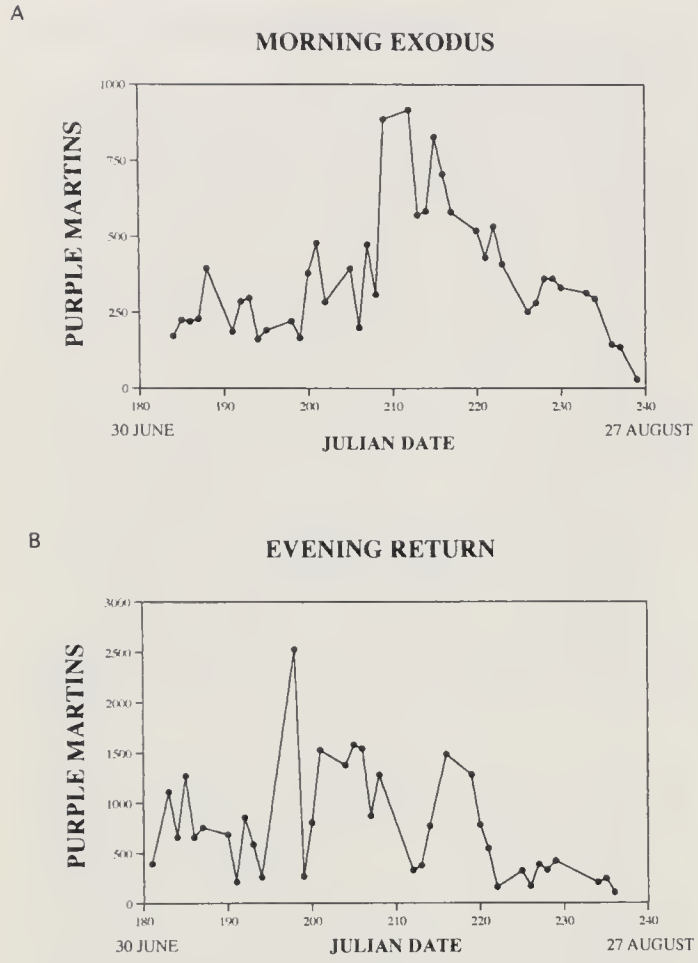

FIG 2. Seasonal changes in visual counts of roosting Purple Martins during (A) morning departures and (B) evening arrivals.

servation point yielding an estimated total roost population (TRP) of 131,752 birds, but on 31 July we counted 916 birds, yielding a peak morning TRP of 701,656 birds. On the last morning census (27 August), we counted only 29 birds (TRP = 22,214). Although evening counts usually were higher than morning counts, numbers of birds returning to the roost also followed a pattern of increase and decline (Fig. 2). The first (30 June), peak (17 July), and last (27 August) evening counts yielded TRPs of 301,804 birds, 1,938,746 birds, and 0 birds, respectively. However, the peak morning count occurred two weeks after the peak evening count and morning counts were not related to evening counts from the previous night ($r^2 = 0.001$, $P > 0.05$, $n = 32$) or the same night ($r^2 = 0.01$, $P > 0.05$, $n = 32$).

DISCUSSION

Timing of flights.—Our observations indicate that flights of Purple Martins from and to pre-migratory roosts are related to levels of ambient light. Purple Martins (Brown and Wolfe 1978, Oren 1980, Hill 1988), Crag Martins (*Ptyonoprogne rupestris*; Elkins and Etheridge 1974), and other species of swallows (Rudebeck 1955, Loske 1984, Skutch 1989, Komar 1997) have been shown previously to enter and exit roosts in response to changing intensities of light. Although endogenous factors likely are a significant influence on the timing of departures and arrivals of birds at roosts (Aschoff 1967), cueing on changing light levels has been suggested as a selective advantage for maximizing time available for feeding (Eastwood et al. 1962, Summers and Feare 1995).

The timing of evening flights was less predictable than morning departures and appeared to be related to date. Across a season the departure or arrival times of the first and last birds at roosts may show greater variation than peaks of departure or arrival (Summers and Feare 1995). In our study, more variation was associated with the times martins first arrived in the vicinity of the roost than when flights were terminated, as was reported previously for other roosting species (Eastwood et al. 1962, Meanley 1965, Bünning 1973, Krantz and Gauthreaux 1975). We suggest that relationships between date and the timing of evening arrivals of martins are related mostly to the large variation associated with these flights.

Spatial pattern of flights.—As with other roosting species (Harper 1959, Eastwood et al. 1962), the omnidirectional departures of Purple Martins that we observed on radar were associated with daily feeding flights (Russell 1996). In contrast, directionally biased patterns of flight on radar are often associated with migration departures (Harper 1959, Richardson and Haight 1970). The strong southerly bias in the annulus and its eventual disappearance during the latter part of August, in conjunction with our declining visual counts, marked increasing fall migration departures and eventual abandonment of the roost.

Among our more surprising results was the long distances Purple Martins flew from the roost. Prior to our study, it was believed that the birds foraged within 10–15 km of the Lake Murray roost (J. Cely, pers. comm.). Brown and Wolfe (1978) suggested that Purple Martins may travel as far as 48 km from

pre-migratory roosts during the day while feeding. Our radar data clearly showed that birds regularly flew almost 80 km and occasionally as far as 100 km from the roost. If the large population size of the roost and thus foraging competition (Caccamise et al. 1983, Summers and Feare 1995) was responsible for the flight distances we observed, a significant relationship should have emerged between the extent of departures and changes in TRP, but it did not. In fact, some of the longest flights occurred early in the season, when TRP was relatively small. Because we did not track individuals, we do not know the ultimate destination of the birds or whether all departing individuals returned the same evening.

Flight directions and speeds.—In marked contrast to the uniform departures of Purple Martins, we observed high variability in the flight tracks of birds arriving at the roost. Even during the peak of arrivals, mean flight direction of the birds was east of the roost. This directional bias and our own incidental observations indicate that Purple Martins return to the roost via specific flight corridors. Use of preferred flight lines often is associated with evening movements to roosts (Eastwood et al. 1962, Meanley 1965, Skutch 1989). After arriving at the roost the birds assembled in a high, circling mass before a final entry at sunset. This pattern is very similar to the phases of "staging" or pre-settling behavior (initial aimless flight, formation of a tight flock near the roost, final descent; Loske 1984) previously described for *Progne* spp. (Brown and Wolfe 1978, Oren 1980, Hill 1988) and other genera of roosting swallows (Bent 1942; Loske 1984, 1986; Skutch 1989, Komar 1997). Flight speeds of departing Purple Martins we recorded on radar (10.8–13.4 m/s) were similar to those reported by Evans and Drickamer (8.45–11.09 m/s; 1994) and Southern (12.1 m/s; 1959).

Weather conditions and roosting flights.—Because Purple Martins apparently respond to some threshold level of ambient light for the cueing of flights from and to the roost, the timing of these movements should vary with daily differences in light levels caused by changing cloud cover (Richardson 1978, Elkins 1983). In our study, cloud cover and atmospheric pressure were the most important weather conditions explaining variation in the timing of roosting flights. Increasing or decreasing light levels reach a given intensity later or earlier, respectively, on days with overcast conditions compared to clear days. Atmospheric pressure is often inversely correlated with the amount of cloud cover (Riehl 1972). The inclusion of other variables into the stepwise models also may have resulted from intercorrelations with cloud cover, atmospheric pressure, or date (Richardson 1978). Because these weather variables were highly intercorrelated, the most that can be assumed is that the birds responded to some aspect of the weather that was interrelated with the significant variables (Richardson 1978). Thus, we view our results as a preliminary explanation of variation in the flight behaviors of roosting Purple Martins, rather than representing causal mechanisms.

Finlay (1976) observed the influence of cloud cover on Purple Martins during the nesting season; the birds departed from nests earlier on clear days than on cloudy days. Also, Elkins and Etheridge (1974) found that Crag Martins returned to roosts up to 2.5 h earlier on overcast or cloudy days. The influence of cloud cover on the extent of martin roosting flights may in part be related to the aerial foraging habits of the birds (Elkins 1983). In two studies of Purple Martin food habits (Spice 1972, Walsh 1978), the intake of airborne insects was negatively correlated with cloud cover. Cloudy weather also was shown to reduce the amount and type of airborne insects taken by Brown-chested Martins (*Phaeoprogne tapera*) in Venezuela (Turner 1984). Additionally, Finlay (1976) reported that during overcast conditions martins appeared to spend more time away from nests, presumably searching for food. It is possible that cloudy conditions forced roosting Purple Martins to travel longer distances in search of prey (Elkins 1983).

Our radar observations that winds aloft displaced the annular departures of Purple Martins indicate that the birds continued to fly with constant headings and speeds, apparently making no correction for drift in spite of their presumed knowledge of the local topography. Similar radar observations were made by Eastwood et al. (1962) of wind displaced departures of European Starlings (*Sturnus vulgaris*) from roosts.

Seasonal changes in total roost population.—The overall increase in TRP through the end of July likely reflects recruitment of local and regional populations after the fledging period (Brown 1997). Although Purple Martins are colonial breeders they nest asynchronously (Brown 1997), and in South Carolina clutches have been observed as early as 11 April and as late as 19 June (Post and Gauthreaux 1989). Thus, it is not surprising that increases in TRP during July occurred gradually. The influx of birds at the roost also occurred too early in the season to be significantly influenced by migration. However, subsequent declines in TRP and changes in flight patterns evident on radar throughout August corresponded with fall migration departures (Hamel 1992, Brown 1997). In the southeastern United States, Purple Martins often depart for South America in early August (Hamel 1992).

Although the roost exhibited a seasonal pattern of growth and decline consistent with pre-migratory assembly, large daily fluctuations in TRP were evident. The accuracy of our TRP estimates depended on the following assumptions: (1) departures and arrivals were equally distributed around the roost, (2) each bird was counted only once during a survey, and (3) birds did not switch among roosts. The annular patterns from radar and uniform flight tracks over the observation point indicate that the first two assumptions probably were met for most morning departures, although some daily variation was likely. In contrast, the large variability and directional bias of evening flights and the lack of relationships between morning and evening counts indicate that the birds did not return to the roost in a uniform manner, and at least early in the evening some birds were counted multiple times. Thus, our evening counts likely did not provide an accurate estimate of the number of martins at the roost on a daily basis.

Another potential source of variation in TRP is movement of birds among roosts. During the present and subsequent (Russell et al. 1998) studies, we discovered another pre-migratory roost of martins 100 km west in Georgia and others within 230 km. Fluctuations in TRP through late July may reflect some switching of birds among roosts on a regional basis, while temporary increases in TRP late in the season also could result from birds encountering the roost during migration from more northerly breeding or roosting sites. Likewise, birds migrating from Lake Murray probably encounter roosts along the Gulf coast (Russell et al. 1998). Although we believe our morning counts provide a good initial assessment of daily changes in TRP and maximum roost size, more accurate estimates will require monitoring roost populations on a regional basis. In part this may require rigorous, labor intensive ground surveys at multiple roost sites (e.g., Caccamise et al. 1983). However, with further refinements in methodology, WSR-88D radar may provide the potential to remotely monitor seasonal and annual changes in roost populations over large geographical areas (Russell and Gauthreaux 1998, Russell et al. 1998).

Why do Purple Martins assemble in pre-migratory roosts?—Large pre-migratory roosts of Purple Martins are neither a recent nor an isolated phenomenon. Wayne (1910), Stone (1937), and Anderson (1965) observed roosts reaching concentrations of at least 100,000, and a well-established roost at Lake Pontchartrain, Louisiana may support 200,000 birds (Rogillio 1989). Some roosts, including Lake Murray and a site in southern Oklahoma (Brown and Wolfe 1978) have been used by martins for 20 years or more (Russell et al. 1998). At least 30 additional major pre-migratory roosts are known to exist in the eastern United States (Russell et al. 1998). Enormous concentrations of roosting Purple Martins also have been documented on their wintering grounds (Oren 1980; Hill 1988, 1993).

Several selective advantages have been proposed for communal roosting behavior: pre-migratory assembly (Allen and Nice 1952, Michael and Chao 1973, Skutch 1989), reduced risk of predation (Lack 1968), more efficient thermoregulation (Williams et al. 1991), enhanced foraging ability through information exchange (Ward and Zahavi 1973, Brown and Brown 1996), and association with super-abundant food supplies or other diurnal activity centers (Caccamise and Morrison 1986, Caccamise 1993). Although the late-summer roosting habits of Purple Martins often are attributed to the need for pre-migratory assembly (Allen and Nice 1952), this seasonal pattern of roosting does not explain the ben-

efits gained by gathering in a large communal assemblage for several weeks prior to migration (Caccamise et al. 1983, Brown 1997). Because the Lake Murray roost is on an island and at least 3 km from the lakeshore the birds likely have little threat from most predators or other disturbances; other large pre-migratory roosts of Purple Martins also are associated with bodies of water (Russell et al. 1998). Additionally, the anti-predator benefits of roosting should reach their maximum value at relatively small population sizes (e.g., < 1000; Pulliam 1973). Although roost advertising is evident in the pre-settling flight behavior of Purple Martins, the omnidirectional departures of the birds and their absence until evening make it unlikely that Lunch Island functions as an information center about local changes in food supply (Skutch 1989, Brown and Brown 1996, Brown 1997).

Our study has quantified aspects of the pre-migratory roosting behavior of Purple Martins that previously were known only from anecdotal accounts (see Brown 1997) or brief comments made during studies of nesting or immediate post-fledging activities (Allen and Nice 1952, Finlay 1971, Brown 1978). Future studies should focus on the costs and benefits of large pre-migratory roosts to Purple Martins and be conducted at scales sufficiently large to monitor spatial and temporal patterns of roosting on a regional basis (Caccamise et al. 1983, Russell et al. 1998). Studies employing radiotelemetry or other tracking methods also are needed to determine the daily and seasonal movements of individual martins, including whether individuals switch among roosts, or commute between roosts and diurnal activity centers (e.g., Caccamise and Morrison 1986, Caccamise 1993).

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AGGRESSIVE RESPONSE OF CHICKADEES TOWARDS BLACK-CAPPED AND CAROLINA CHICKADEE CALLS IN CENTRAL ILLINOIS

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ABSTRACT.—Aggressive responses of Black-capped (*Poecile atricapillus*) and Carolina chickadees (*Poecile carolinensis*) to heterospecific and conspecific vocalization playbacks were measured across a historic contact zone in east-central Illinois to determine the magnitude of interspecific aggression. Within the traditional Carolina Chickadee range, chickadees responded more aggressively towards Carolina Chickadee calls than Black-capped Chickadee calls. Within the traditional Black-capped Chickadee range, chickadees did not respond to either vocalization significantly more than the other. The aggressive response towards presumed heterospecific vocalizations for all chickadees was marginally more aggressive closer to the contact zone. Thus, we conclude that interspecific aggression may not act as a gap producing mechanism between chickadee ranges. *Received 24 Nov. 1998, accepted 31 March 1999.*

Black-capped (*Poecile atricapillus*) and Carolina (*Poecile carolinensis*) chickadees are extremely similar in appearance, behavior, and ecology (Brewer 1963, Johnston 1971, Merritt 1978). They occupy largely parapatric breeding ranges, although there are a few narrow zones of overlap. Interspecific encounters and recognition of heterospecifics are common in these overlap areas (Ward and Ward 1974). Interspecific territoriality in chickadees is rare except with other chickadees in contact zones (Brewer 1963, Smith 1993). Interspecific territoriality may arise through the competition for limited resources, which may contirbute to a competitively-induced gap between Black-capped and Carolina chickadee ranges (Tanner 1952, Slade and Robertson 1977).

We measured the level of aggression exhibited by chickadees across a historic contact zone in Illinois defined by Brewer (1963) to test the role of interspecific aggression as a range segregating mechanism. We hypothesized that responses towards the conspecific vocalization would be more aggressive than those to heterospecific vocalizations. We also hypothesized that levels of aggression to heterospecific vocalizations would be greatest closer to the contact zone and weaker away from the contact zone. We expected this response because closer to the zone of overlap chickadees would have more encounters with congeners and therefore should exhibit more aggressive territorial defense if interspecific aggression is used to maintain range boundaries.

METHODS

Study area.—Our 5 study sites formed a transect across the historical contact zone for chickadees in east-central Illinois (Fig. 1). The distance from the midline of the contact zone varied for each study site (Shelbyville 10 km, Douglas Hart 22 km, Fox Ridge 40 km, Lincoln Trail 58 km, Sangchris 65 km). Sangchris State Park and Shelbyville State Park were located in traditional Black-capped Chickadee range. Fox Ridge State Park, Douglas Hart Nature Center, and Lincoln Trail State Park were located in traditional Carolina Chickadee range. Study sites were visited weekly.

Playback experiments.—Two chickadee calls and one White-breasted Nuthatch (*Sitta carolinensis*) vocalization were used in this experiment. A playback tape (Maxell UDII 60 minutes) was made for each vocalization on a Magnavox FA9403 dual recording stereo system. Each tape had a call rate of 18 calls/minute. Vocalizations of both chickadee species and the White-breasted Nuthatches were taken from the Peterson Guide to Bird Songs® (Peterson 1983). One call of each species was used for all trials. This seemed reasonable given that differences between species calls are much greater than variation of calls within a species. Vocalizations were played to subjects on a Panasonic FW18 dual speaker casscttc recorder.

Playbacks were used to test the abilities of chickadees to discriminate between conspecific and heterospecific vocalizations (Emlen et al. 1975). Several researchers have shown that chickadees respond to conspecific songs more than to heterospecific songs (Hill and Lein 1989, Merritt 1978, Robbins et al. 1986b,

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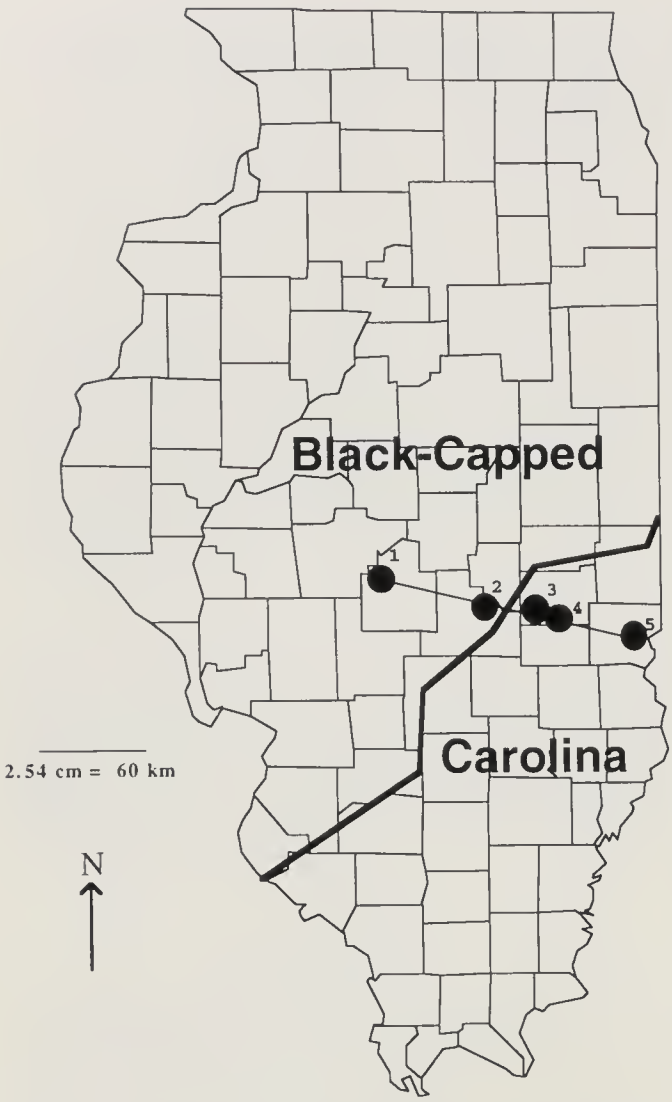

FIG. 1. Map of the study sites. Dark line indicates the historic contact zone across east-central Illinois (from Brewer, 1963). North of the contact zone represents Black-capped Chickadee range and south of the contact zone represents Carolina Chickadee range. Study sites are (1) Sangchris State Park, (2) Shelbyville State Park, (3) Douglas Hart Nature Center, (4) Fox Ridge State Park, and (5) Lincoln Trail State Park.

Ward and Ward 1974). The *chick-a-dee* call was used in this study because it contains sufficient information that can potentially be used by chickadees for individual recognition (Mamman and Nowicki 1981, Smith 1991). These calls tend to be short, less musical, less variable, and relatively specialized for particular functions such as alarm or changing the spacing between individuals (Smith 1991). The playback of *chick-a-dee* calls may elicit elevated calling rates (Nowicki 1983) by simulating intruding males (Hill and Lein 1989, Shackleton et al. 1992), and therefore would measure any differences in aggression levels between vocalization type.

Playback experiments were conducted 08:00–12:00 CST, 1 May–31 July 1995. Two different paired playback trials were conducted. One trial type consisted of broadcasting Black-capped and Carolina *chick-a-dee* call to chickadees in all study sites. The second trial type consisted of playing both a randomly-selected chickadee call (Black-capped or Carolina) and a White-breasted Nuthatch vocalization. This second trial type was played every third trial at each study site. Nuthatches were used because chickadees should be familiar with this vocalization through winter flock association. Therefore, the responses to the nuthatch vocalizations gave us a baseline level of aggression to compare to the responses to chickadee vocalizations.

Playback trials were conducted by slowly walking around the study site until chickadees were detected. Trials were conducted by approaching a single bird as close as possible without visibly agitating it. Only data that fit the following criteria were used: (1) the focal bird could be approached within 15 m, and (2) weather conditions matched those required for the Breeding Bird Survey (Robbins et al. 1986a). Each bird was exposed to only one trial (either a two-chickadee trial or a chickadee-nuthatch trial), and specific areas within each study site were used for only one trial to avoid influencing neighboring chickadees. The minimum distance between trial locations was 500 m and was usually over 1000 m. Vocalizations were played for 2 minutes with a 5 minute silent period between the two sets of vocalizations. The silent period allowed the focal bird to return to normal activity after being exposed to the first vocalization. The order of the two vocalizations were alternated to reduce bias (Kroodsma 1989, Lampe and Baker 1994, Ward and Ward 1974).

Statistical analyses.—The degree of aggression by the focal bird was quantified based on its behavior during the two-minute trial period (Table 1). The identity of species at each study site was assumed to be that of historic record, although the possibility of hybridization may render this assumption invalid. However, all analyses were conducted without regard to species identity. Response scores were analyzed by paired *t*-tests. To compare all chickadee calls combined to nuthatch vocalizations, one trial per site was used and all sites were pooled together. The relationships between mean aggressive response and both date and distance to the contact zone were analyzed by Pearson Correlation Analysis (SAS Institute 1994).

RESULTS

Chickadees responded more aggressively to Black-capped and Carolina chickadee calls combined than to songs of White-breasted Nuthatches ($t = 4.6$, df = 9, $P < 0.001$; Fig. 2). Chickadees also responded more aggressively to each chickadee species call separately than to White-breasted Nuthatch vocalizations (Black-capped: $t = 8.9$, df = 4, $P < 0.001$; Carolina: $t = 5.65$, df = 4, $P < 0.005$; Fig. 2).

There was no significant difference in aggressive response to Carolina calls versus Black-capped chickadee calls ($t = 1.06$, df = 33, $P > 0.05$; Fig. 3). Chickadees within tra-

TABLE 1. Categories of behavioral responses for Black-capped Chickadees (*Poecile atricapillus*) and Carolina Chickadees (*Poecile carolinensis*) to playbacks of conspecific and heterospecific calls. Categories were derived by combining information from Brindley (1991), Censky and Ficken (1982), Ficken and Wiese (1984), Popp and coworkers (1990), Schroeder and Wiley (1983), and Shackleton and coworkers (1992). The categories run on a 0–10 scale with 10 being the most aggressive.

Category	Behavior
10	Flights <2 m from tape player, wing twittering
9	Flights 2–5 m from tape player
8	Flights <5 m from tape player, >2 gargles
7	Flights <5 m from tape player, <2 gargles
6	Flights 5–10 m from tape player, >4 calls made
5	Flights 5–10 m from tape player, <4 calls made
4	Flights 5–10 m from tape player, songs elicited
3	Flights >10 m from tape player, calls elicited, some gargling
2	Flights >10 m from tape player, songs elicited
1	minimal interest shown in recording, moving away from area
0	no interest, left area during trial

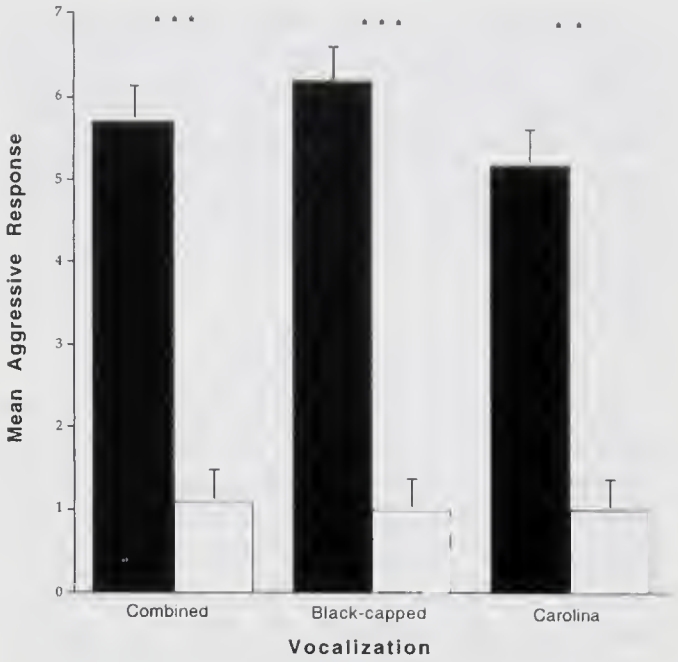

FIG. 2. Mean aggressive response of chickadees in paired Black-capped Chickadee-nuthatch (n = 5), Carolina Chickadee-nuthatch (n = 5), and for all trials combined (n = 10). Dark bars represent the response to chickadee calls and light bars represent the response to nuthatch vocalizations. ** $P < 0.01$, *** $P < 0.001$.

ditional Black-capped Chickadee range did not respond significantly more aggressively to Black-capped calls than to Carolina calls (t = 1.35, df = 12, $P > 0.05$; Fig. 3). However, chickadees within traditional Carolina Chickadee range were more aggressive towards Carolina calls than Black-capped calls (t = 2.75, df = 20, $P < 0.01$; Fig. 3).

When sites were analyzed separately, only chickadees at Fox Ridge State Park responded significantly more aggressively towards a given chickadee vocalization. Chickadees at Fox Ridge responded more aggresssively to Carolina calls than Black-capped chickadee calls (t = −2.74, df = 8, $P < 0.03$; Fig. 3).

Aggressive responses towards both Black-capped (r = −0.71, n = 5) and Carolina chickadee vocalizations (r = −0.29, n = 5) increased at decreasing distances to the contact zone, although neither was statistically significant ($P > 0.05$). With both species combined, the relationship (r = −0.49, P = 0.08, n = 10) was still not significant ($P > 0.05$). Futhermore, chickadees did not show a sea-

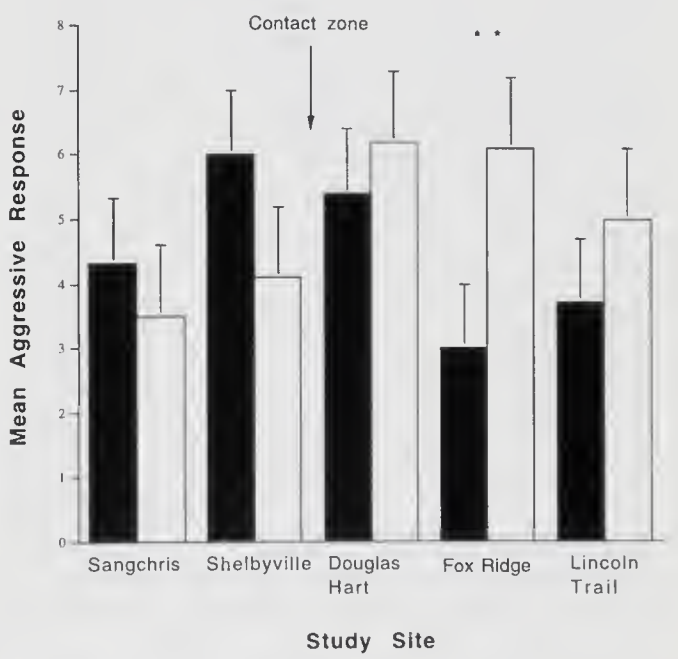

FIG. 3. Mean aggressive response of chickadees to Black-capped and Carolina *chick-a-dee* vocalizations at all study sites. Dark bars represent the response to Black-capped Chickadee calls and light bars represent the response to Carolina Chickadee calls. The study sites are arranged from West to East and the contact zone is noted between Shelbyville and Douglas Hart. (Sample sizes were 6, 7, 5, 9, 7 respectively; * * $P < 0.05$.)

sonal difference in response, when all trials were combined ($r = -0.12$, $P > 0.05$, $n = 36$). Separately, there was no relationship between mean aggressive response to either Black-capped or Carolina Chickadee vocalizations and date ($r = -0.28$, $P > 0.05$, $n = 18$ and $r = 0.05$, $P > 0.05$, $n = 18$, respectively).

DISCUSSION

The fact that chickadees responded more aggressively to chickadee calls than nuthatch vocalizations indicated that chickadees were able to discriminate between congeneric and heterogeneric vocalizations (Fig. 2). These results are consistent with other studies that suggest that interspecific territoriality in chickadees is rare except with other chickadees in contact zones (Brewer 1963, Smith 1993).

We found that within the traditional Carolina Chickadee range, chickadees responded more aggressively to presumed conspecific calls. This is consistent with the results of studies on buntings in allopatric populations (Emlen et al. 1975) and in tropical birds in Peru (Robinson and Terborgh 1995). Several researchers found that chickadees responded more aggressively to their own song type than to songs of other chickadee species except in the contact zone where they responded aggressively to both conspecific and heterospecific song types (Ratcliffe and Weisman 1986, Robbins et al. 1986b). This differs from our results at one site. Chickadees at Fox Ridge State Park showed significantly more aggression to presumed conspecific vocalizations than towards heterospecifics. Overall, chickadees clearly responded more aggressively to chickadee calls than nuthatch calls with little difference between presumed hetero- and conspecific chickadee calls. This suggests that chickadees may either not perceive nuthatches as a competitive threat or that chickadees near contact zones may not distinguish between chickadee species calls.

We did not get the predicted increase in aggression towards heterospecifics closer to the contact zone. It is possibile that the maximum distance from the contact zone used in this study was not far enough to detect any significant differences in aggression. This would suggest that chickadees across the area are familiar with congeners. Merritt (1981) suggested that individual chickadees expand and contract their ranges seasonally. As the ranges of these species approach each other, cognizance of the heterospecific vocalization should increase (Ward and Ward 1974). At increasing distances from the contact zone, there could be a point where the mean aggressive responses would be significantly lower than closer to the contact zone.

Two other possible explanations exist for the aggression shown towards a presumed heterospecific call within species' ranges: misdirected aggression and the presence of hybrids. Misdirected aggression could arise from mistaken identity (Murray 1971, 1981). This is possible because the vocalizations of both species are similar and variable between individuals, and we used only one example of each vocalization type in this experiment (Mammen and Nowicki 1981, Smith 1991). However, this aggression could be intentional, because response to heterospecific calls may promote recognition and facilitate heterospecific spacing (Emlen et al. 1975, Merritt 1981, Robinson and Terborgh 1995). Hybridization may be more common in contact zones than previously thought (Brewer 1963, Johnston 1971, Rising 1968, Robbins et al. 1986b, Ward and Ward 1974). Thus, the lack of species specific aggressive responses could be the result of the presence of hybrids that are familiar with and respond similarly to calls of both species. If hybridization is the cause for the observed interspecific aggression, it is likely that interspecific territoriality may not act as a gap producing mechanism. Gaps between Black-capped and Carolina chickadee ranges may occur if hybrids within these gaps had severely reduced fitness (Brewer 1963). However, other factors may cause gaps. One such example is the lack of suitable habitat in gaps areas (Grubb et al. 1994).

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USE OF SONG TYPES BY MOUNTAIN CHICKADEES (*POECILE GAMBELI*)

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ABSTRACT.—We investigated the composition and function of individual song repertoires in Mountain Chickadees (*Poecile gambeli*) in Alberta, Canada. Individual males had repertoires of 4–7 song types, but three types made up 90% of all songs. We tested and rejected the hypothesis that all song types convey the same behavioral messages. Different song types were associated with different behavioral situations. Males used 3-note songs predominantly during undisturbed singing and 2-note songs predominantly during non-aggressive activity. Three-note songs with each successive note lower pitched were associated with male–male interactions. We suggest that different song types convey messages indicating different levels of aggression by the singer. The function of individual repertoires in Mountain Chickadees appears to be similar to that of other North American chickadees and titmice, with different song types having different communicative functions. *Received 7 Aug. 1998, accepted 11 Feb. 1999.*

Although individuals of some species of songbirds sing only one type of song (Searcy 1983), males of many species possess repertoires comprising a number of discrete categories of songs, or song types (Dodson and Lemon 1975). The significance of song repertoires has been the subject of much research and speculation (reviewed by Krebs and Kroodsma 1980, Kroodsma 1982, Kroodsma and Byers 1991, MacDougall-Shackleton 1998).

Most species of the genera *Parus, Poecile,* and *Baeolophus* have individual song repertoires (Hailman 1989), although the role of repertoires appears to differ among species [these closely-related genera were formerly lumped as *Parus* (American Ornithologists' Union 1997)]. Individual male Great Tits (*Parus major*) may use different song types in sequence with no apparent change in the external situation (Hinde 1952), suggesting that all song types convey the same messages. Consequently, Great Tits have been used to test many of the hypotheses that suggest that overall repertoire size is important (e.g., Krebs 1976, 1977; McGregor et al. 1981; Baker et al. 1986; Lambrechts and Dhondt 1988). In contrast, other species, such as the Blue Tit (*Parus caeruleus*), the North American titmice (*Baeolophus*), and some of the North American chickadees (*Poecile*), seem to possess song types that convey different messages (Smith 1972, Dixon and Martin 1979, Gaddis 1983, Schroeder and Wiley 1983, Bijnens and Dhondt 1984, Johnson 1987).

We examine the role of individual repertoires of Mountain Chickadees (*Poecile gambeli*). Mountain Chickadees sing relatively simple songs consisting of 2–6 whistled notes, with any number of these notes shifted to frequencies lower than the others (Hill 1987). Song types are defined easily by variation in number and pitch of notes; individual repertoires consist of 3–5 song types (Hill and Lein 1989). Although no studies have investigated whether Mountain Chickadees can differentiate among song types, this seems probable because closely related Black-capped Chickadees (*Poecile atricapillus*) distinguish among songs varying in note number and pitch (Ratcliffe and Weisman 1986; Weisman and Ratcliffe 1989).

We documented song variation and singing behavior of male Mountain Chickadees during the breeding season. Our null hypothesis was that all song types of the Mountain Chickadee convey the same behavioral messages, and thus the song type that a male sings would be independent of the situation in which it is used. The alternate hypothesis was that song types convey different messages and thus certain song types would have a higher probability of being sung in specific situations.

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METHODS

The study was conducted at the Barrier Lake site (51° 00′ N, 115° 00′ W) of the University of Calgary's Kananaskis Field Stations in the Kananaskis Valley of the Rocky Mountains of southwestern Alberta. The forest inhabited by Mountain Chickadees is dominated by trembling aspen (*Populus tremuloides*), white spruce (*Picea glauca*), and lodgepole pine (*Pinus contorta*). Mountain Chickadees are secondary cavity-nesters, using pre-existing cavities such as natural crevices or deserted nests of other cavity-nesting birds (Hill 1987, pers. obs.). In southwestern Alberta, Mountain Chickadees start to search for suitable nesting cavities during April (Hill 1987, pers. obs.). Nest-building occurs in early May. Incubation starts near the end of May and lasts about 14 days. The nestling period generally lasts 18–21 days (Dahlsten and Copper 1979) but may be as short as 14 days (pers. obs.). Nestlings fledge during the last week in June and early July.

Mountain Chickadee songs, and information on the situations of song use, were recorded from April to July 1993. Data were collected from 11 males, of which 7 were marked with a unique combination of colored plastic leg bands. We could identify unbanded males because males in adjacent territories were banded; we also used territorial location, use of favorite singing sites, or association with a particular nest cavity to identify unbanded males. All males except one foraged frequently with one other Mountain Chickadee and therefore were presumed to be mated. Because Mountain Chickadees defend their entire home range (Hill 1987), we determined the extent of a male's territory by noting areas in which he was found regularly. Observations of aggressive interactions between males helped to confirm the locations of territorial boundaries.

It was impossible to sample songs of all individuals in one day, but usually each individual was observed at least once in a three-day period. Observations occurred between 04:00 and 12:00 (MST), the period when chickadees are most active. An observation period began when a male started to sing and lasted from a few minutes to over an hour, depending on how long the individual sang. Songs and verbal descriptions of the different elements of the situation during singing were recorded onto Sony C-90HF cassette tapes using AKG D190E or Sony ECM-33P microphones, Sony PBR-330 parabolic reflectors, and Sony TCM-5000 or Sony TCM-5000EV tape recorders.

All recordings were made by either MOW or a field assistant. Before working independently, the field assistant accompanied MOW during 15 observation periods to ensure that both observers were making comparable observations. We did not notice chickadees engaging in behaviors directed at the observer during any of the observation periods, so we believe that the effect of our presence was minimal.

We recorded three elements of the situation while males were singing. (1) Behavior of the singer: a. undisturbed (i.e., singing while stationary and not engaged in other activities); b. engaged in non-aggressive activities (e.g., foraging, preening, feeding nestlings, etc.); c. engaged in aggressive activities (i.e. countersinging with or chasing territorial neighbors). (2) Position on territory: a. within 50 m of the nest site; b. away from the nest site. (3) Location of mate: a. present in the vicinity of the singer; b. absent from the vicinity. Each song was assigned to a particular situation. If the situation changed while the male was singing, then songs recorded before the change were assigned to the first situation, and songs recorded after the change assigned to the second situation. Nests of six pairs were found, allowing us to also assign songs for these males to particular breeding stages (nest search/build, egg-laying, incubation, or nestling).

Mountain Chickadees often were out of sight when in the tops of coniferous trees. We assumed that songs given during such intervals were in the same situation as the last song given prior to disappearance. However, if a subject was out of sight for more than 5 minutes, we recorded its behavior for that interval as unknown.

We categorized different song types by variation in number of notes and relative pitch of notes within a song. These two features showed the most obvious variation among songs and were relatively easy to distinguish by ear. We confirmed these classifications by examining audiospectrographs of many songs using SIGNAL bioacoustical analysis software (Engineering Design, Belmont, Massachusetts). Transcriptions of recordings were made using OBSERVER software (Noldus Information Technology, Wageningen, The Netherlands).

We examined separately the relative importance of number of notes in a song and the pitch of notes within a song. To determine the influence of number of notes, we combined all song types with the same number of notes regardless of the pitch of the notes within the song. Statistical tests were performed only for 2-note and 3-note songs because sample sizes for songs with 1 note and 4 notes or more were too small. To examine the influence of pitch, statistical tests were performed only for "common 3-note songs" and "descending 3-note songs" (see descriptions in Results). Sample sizes of other song types with variations in pitch were too small for statistical testing.

If different song types are not used in different situations, one would predict that a particular song type should occur in a specific situation at the frequency expected if song types are used at random. To examine the influence of note number in songs, we calculated χ^2 values for 2×2 contingency tables of either the relative number of 2-note songs and all other song types compared between specific situations of use, or the relative number of 3-note songs and all other song types compared between specific situations of use. To examine the influence of pitch in songs, we calculated χ^2 values for 2×2 contingency tables of the number of common 3-note songs and descending 3-note songs compared between specific situations of use. The independent event in all contingency tables was a single song.

We conducted a separate contingency analysis for each individual for every situation of use. We were not able to record all individuals in different situations. Consequently, the number of individuals used in each comparison varied from four to seven. We combined the results of individual contingency analyses using a test described by Cochran (1971:151). This test accounts for differences in direction of response among individuals and can be used even if there is a wide range of sample sizes and probabilities among individuals. The test calculates a z-value that can be compared to the normal distribution to determine significance, with non-significant results indicating that the song types are independent of the situation of use. The sign of the z-value indicates the direction of deviation from the expected.

Most statistical tests were performed using STATISTIX 3.5 for Windows (Analytical Software, St. Paul, Minnesota). Differences at an $\alpha \leq 0.05$ were considered to be significant.

RESULTS

Composition of song repertoires.—We recorded an average of 1,501 songs (± 435 SE; range = 222–4,372) from each of the 11 focal males, with an individual male being recorded an average of 15.1 days (± 2.2; range = 6–28). Average total repertoire size was 7.4 song types (± 0.3; range = 6–9). However, song types used rarely by an individual may have been "accidental" productions rather than regular elements in the repertoire. Excluding song types that represented less than 1% of the total songs for an individual, the average repertoire size was 5.1 song types (± 0.3; range = 4–7). There was no relationship between the number of songs recorded from an individual and the estimated size of his repertoire (all song types: Spearman $r = 0.36$, $P > 0.05$, $n = 11$; song types > 1%: Spearman $r = -0.27$, $P > 0.05$, $n = 11$), indicating that all repertoires were sampled adequately.

"Common 3-note songs" (3-note songs with the last two notes lower in pitch than the first note, Fig. 1A), "common 2-note songs" (2-note songs with the second note lower-pitched, Fig. 1B), and "descending 3-note songs" (3-note songs with each successive note at least 200 Hz lower in pitch than the previous note, Fig. 1C) were the prevalent song types. The most-frequent song type was common 2-note song for 5 of the 11 focal males, common 3-note song for 4 males, and descending 3-note song for 2 males. All males sang these three song types, but for three individuals < 4% of total songs recorded were descending 3-note songs. All other variants had frequencies of < 12% of an individual's repertoire, including 2-note and 3-note songs with all notes of the same pitch (i.e., within 200 Hz of one another; Figs. 1D, 1E) and songs with four or more notes (Fig. 1F). Wiebe (1995) gives details of frequencies of use of song types by each focal male and the use of 2-note songs, common 3-note songs and descending 3-note songs, in different situations by individual males. These data are summarized in the following sections.

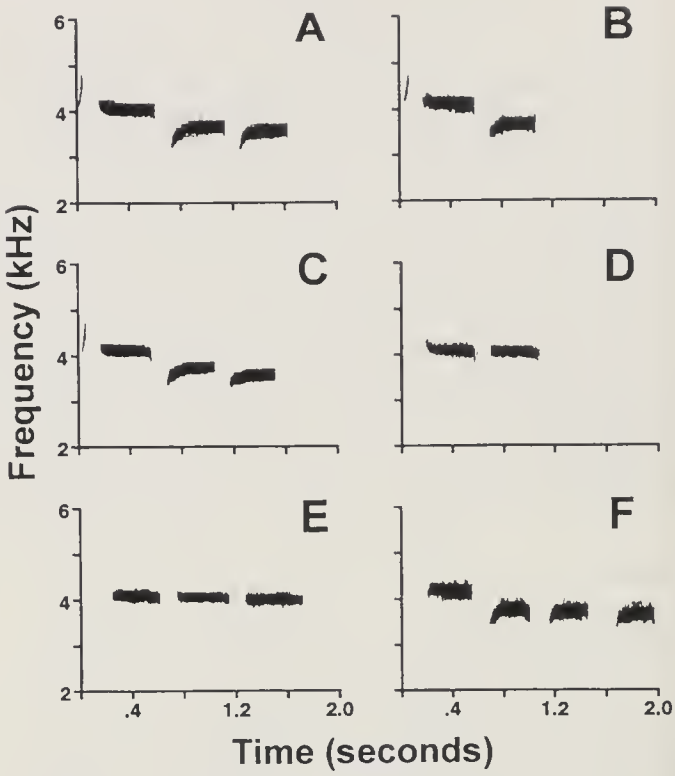

FIG. 1. Audiospectrograms of song types most commonly used by Mountain Chickadees on the study area. A. Common 3-note song. B. Common 2-note song. C. Descending 3-note song. D. 2-note song with both notes the same pitch. E. Three-note song with all notes the same pitch. F. Typical 4-note song. All high-quality recordings of songs had the short, upswept note at the beginning of the song that is present in the common 3-note, the common 2-note song, and the descending 3-note song shown in this figure.

Variation in song use among breeding stages.—Two-note and 3-note songs were not used at random during many breeding stages, although there was much individual variation in the relative use of these song types within all stages (Tables 1, 2). Likewise, common and descending 3-note songs were not used at random during different stages and there was also much individual variation (Table 3).

TABLE 1. The use of 2-note songs by male Mountain Chickadees in various situations, compared to all other song types. Columns headed "All males" refer to combined analysis of contingency tables for individual males. Columns headed "Individual males" indicate numbers of contingency tables for individual males with significant departures from expectations.

Situation	All males				Individual males Preferred song type		
	n	Preferred song[a]	*z*-value	*P*	2-note	Other	None
Nest searching/building stage	5	Other	−6.77	<0.01	2	3	0
Egg-laying stage	6		+1.86	0.06	3	1	2
Incubation stage	6	2-note	+5.99	<0.01	3	1	2
Nestling stage	4	Other	−2.30	0.02	1	1	2
Near nest	6	2-note	+3.94	<0.01	4	0	2
Mate present	7	Other	−2.45	0.01	1	3	3
Undisturbed singing	7	Other	−9.11	<0.01	0	5	2
Male-male interaction	6		−0.22	0.83	0	0	6

[a] Indicates that 2-note songs were used significantly more frequently (2-note) or less frequently (Other) than expected in that situation. A blank indicates no significant deviation from expected frequencies.

Variation in song use among behavioral situations.—When singing near the nest site, males used 2-note songs significantly more frequently (Table 1) and 3-note songs significantly less frequently (Table 2) than expected. This pattern also is reflected in the song types used preferentially by individuals. Common 3-note songs were less frequent than expected (and descending 3-note songs more frequent) when males were singing near the nest, although there was much individual variation (Table 3).

Males sang 2-note songs significantly less frequently than expected in the presence of their mates, as indicated by the combined analysis and by the preferred song types of individuals (Table 1). Common 3-note songs were used significantly more frequently than expected in this situation, with five of seven individuals using common 3-note songs preferentially (Table 3).

When engaged in undisturbed singing, in comparison to singing while engaged in another non-aggressive activity such as foraging, 2-note songs were used significantly less frequently (Table 1), and 3-note songs significantly more frequently (Table 2) than expected. Song type preferences of individuals are entirely concordant with this overall pattern. Frequencies of common and descending 3-note songs did not differ from expectations during undisturbed singing (Table 3).

During male–male interactions, common 3-note songs were used significantly less frequently, and descending 3-note songs significantly more frequently, than expected (Table 3). Three of five males showed significant preferential use of descending 3-note songs

TABLE 2. The use of 3-note songs by male Mountain Chickadees in various situations, compared to all other song types. See Table 1 for an explanation of the format.

Situation	All males				Individual males Preferred song type		
	n	Preferred song[a]	*z*-value	*P*	3-note	Other	None
Nest searching/building stage	5	3-note	+5.71	<0.01	3	2	0
Egg-laying stage	6		−0.76	0.45	1	3	2
Incubation stage	6	Other	−5.55	<0.01	0	3	3
Nestling stage	4		+1.55	0.12	1	1	2
Near nest	6	Other	−4.82	<0.01	0	4	2
Mate present	7		+1.48	0.14	3	2	2
Undisturbed singing	7	3-note	+10.34	<0.01	5	0	2
Male-male interaction	6		+0.59	0.56	0	1	5

[a] Indicates that 3-note songs were used significantly more frequently (3-note) or less frequently (Other) than expected in that situation. A blank indicates no significant deviation from expected frequencies.

TABLE 3. The use of common 3-note songs by male Mountain Chickadees compared to the use of descending 3-note songs in various situations. See Table 1 for an explanation of the format.

Situation	All males				Individual males Preferred song type		
	n	Preferred song[a]	*z*-value	*P*	Common 3-note	Descending 3-note	None
Nest searching/building stage	4	Common	+8.73	<0.01	3	1	0
Egg-laying stage	6	Common	+8.36	<0.01	3	2	1
Incubation stage	5	Descending	−10.73	<0.01	2	3	0
Nestling stage	4	Descending	−5.65	<0.01	1	2	1
Near nest	6	Descending	−4.35	<0.01	3	2	1
Mate present	7	Common	−6.56	<0.01	5	1	1
Undisturbed singing	4		+0.94	0.35	2	1	1
Male-male interaction	5	Descending	−6.72	<0.01	0	3	2

[a] Indicates the 3-note song type that was used significantly more frequently than expected in that situation. A blank indicates no significant deviation from expected frequencies.

during this situation whereas none used common 3-note songs preferentially.

DISCUSSION

Individual song repertoires.—Excluding infrequent song types, males had individual repertoires of 4–7 song types. Hill and Lein (1989) estimated a slightly smaller repertoire size of 3–5 song types. However, they sampled songs less intensively and may not have recorded enough songs to obtain complete song repertoires for all individuals.

Other researchers imply that the most common song type of Mountain Chickadees is a 3-note song with all notes of the same pitch (Gaddis 1985, Hailman 1989, Hill and Lein 1989). In contrast, we found that males in our study rarely sang songs of this type. We are unable to explain this difference, but it may support Gaddis' (1985) suggestion of geographical variation in Mountain Chickadee songs.

Use of song types in different situations.—Our analyses of song length grouped different song types with the same numbers of notes into a single category, possibly obscuring some patterns in the use of different song types. However, because almost all 2-note songs recorded were common 2-note songs, the results from analyses of all 2-note songs would be almost identical to results using only common 2-note songs. Almost all 3-note songs recorded were either common or descending 3-note songs. Any differences between these song types that were obscured in the song length analyses should be revealed in the song pitch analyses.

Different song types had significant associations with different breeding stages. However, there was also much individual variation in all stages, with different males using different songs preferentially during the same breeding stage. This suggests that although the z-values were significant statistically, the results may not be meaningful biologically. Different song types are probably not signaling messages about the breeding stage of the singer. Instead, different breeding stages may be associated with other situations that are more relevant biologically to the messages of the song type.

The number of notes in songs of Mountain Chickadees was associated significantly with location relative to the singer's nest. All individuals showing significant preferences either used more 2-note songs near the nest than away from it, or more 3-notes away from the nest than near it. Some other studies on songbirds also have found that males sang different song types depending on their territorial location (e.g., Lein 1978, Weary et al. 1994). Although pitch of the last note in 3-note songs was associated with location relative to the nest, this association is weak because of the large degree of individual variation.

In Mountain Chickadees, the tendency to sing 2-note songs near the nest and 3-note songs away from the nest may be influenced by factors other than just the singer's location. Males were more likely to engage in non-ag-

gressive activities while singing near the nest than when singing away from the nest, suggesting that location relative to the nest and male behavior were related. Although note number may communicate some information about the singer's location, these factors may be related only indirectly and the association between male behavior and note number may be more important biologically.

Different song types were associated with the presence or absence of the singer's mate. Other researchers (e.g., Temrin 1986, Staicer 1989) have claimed that song types used preferentially in the presence of females have a greater intersexual function. One methodological problem in our study is that a female may have been recorded as absent when she actually was nearby in the nest hole, but not visible to the observer. Two-note songs and descending 3-note songs, which were positively associated with the absence of the female, were also positively associated with the nest site. Furthermore, in most cases singers did not seem to be directing song specifically at females. Males sometimes sang low-volume, "quiet" songs, usually of 1 or 2 notes, when approaching nests to feed incubating mates. Although such songs may be directed specifically at females, we never observed normal volume songs used in this manner. Therefore, we are hesitant, without further experimental study, to suggest that common 3-note songs have a greater intersexual function than do 2-note songs and descending 3-note songs.

The behavior of singing males was associated with the number of notes in the song, but not with pitch. Two-note songs were positively associated with singing while engaged in non-aggressive activity and 3-note songs were positively associated with undisturbed singing. Although not all males had individual results that were significant, all males showed this trend.

We suggest that 3-note songs signal a higher motivation level of the singer to sing than do 2-note songs. If so, 3-note songs might indicate that the singer is more willing to engage in some of the agonistic actions associated with singing in Mountain Chickadees, such as countersinging bouts or interacting with other males at the edge of the territory to confirm boundaries. Thus, 3-note songs could convey more aggressive messages than 2-note songs.

Male–male interactions in Mountain Chickadees were associated with changes in pitch of notes in the song. Because most males were more likely to sing common 3-note songs when apparently unprovoked by another bird's activities than during interactions with rival males, this song type may function in spontaneous advertisement of the territory. Descending 3-note songs were associated with male-male interactions and it is probable that lowering the pitch of the last note in 3-note songs may convey some message to the rival. Other researchers have suggested that song types associated with male–male interactions probably convey more aggressive messages than do other song types (e.g., Nelson and Croner 1991). Interactions between males are situations of high levels of agonistic stimulation for Mountain Chickadees and so they may be more likely to use songs that convey stronger aggressive tendencies at this time. Thus, descending 3-note songs may convey more aggressive messages than common 3-note songs.

Comparison to closely-related species.— Our findings suggest that the function of individual repertoires in Mountain Chickadees is similar to that of other North American chickadees and titmice, with different song types used in different situations and appearing to have different communicative functions. Three species of North American titmice have certain song types that are used predominantly in male–male interactions (Gaddis 1983, Schroeder and Wiley 1983, Johnson 1987). These are probably similar in function to the descending 3-note song of the Mountain Chickadee, which is also used in male–male interactions. The Bridled Titmouse (*Baeolophus wollweberi*) has one song type used predominantly in spontaneous advertisement of territory (Gaddis 1983), and we found that the common 3-note song of the Mountain Chickadee is used predominantly in undisturbed singing. Schroeder and Wiley (1983) suggested that different song types of the Tufted Titmouse (*B. bicolor*) convey different levels of aggression by the singer. This corresponds to our suggestion that, in Mountain Chickadees, descending 3-note songs, common 3-note songs, and 2-note songs indicate

high, intermediate, and low levels of aggression, respectively.

There are also some differences in the manner in which titmice and Mountain Chickadees use songs. For instance, the Bridled Titmouse has a song type used predominantly in long-distance countersinging (Gaddis 1983). We did not find any song type in Mountain Chickadees that was used in this manner, although it is possible that some songs that we categorized as "undisturbed" singing may have actually been in response to far away song that was inaudible to the observer. Johnson (1987) noted that the Plain Titmouse (*Baeolophus inornatus*) was more likely to use some song types in situations related to nesting activities. Although 2-note songs were associated with close proximity to the nest, there was no indication that Mountain Chickadees were using these songs in any way that was related specifically to nesting activity.

Carolina Chickadees (*Poecile carolinensis*) have one song type associated with countersinging that is thought to be a more aggressive song type (Smith 1972). This song type could be similar in function to descending 3-note songs given by Mountain Chickadees during male–male interactions. However, Smith (1972) also observed that Carolina Chickadees were more likely to use this aggressive song type while patrolling territorial boundaries whereas we did not note any strong association between descending 3-note songs and territorial boundaries.

Pitch may be an important cue in coding information in the songs of both Mountain and Black-capped chickadees, but the two species differ in how they vary the pitch of their songs. Unlike Black-capped Chickadees, which shift the entire song downward in pitch, Mountain Chickadees shift individual notes in a song to a lower pitch. Black-capped Chickadee songs shifted downward in pitch were observed during countersinging between males in the field and in response to playback in both wild and captive birds (Ratcliffe and Weisman 1985, Hill and Lein 1987). Mountain Chickadees 3-note songs, with the last note lower in pitch (descending 3-note songs), were associated with male–male interactions whereas 3-note songs with the last two notes of the same pitch (common 3-note songs) were associated with the less-aggressive situation of territorial advertisement. In both species, pitch seems to be lowered during more aggressive situations. Morton (1977) suggested that calls of low pitch indicate higher aggressiveness by the signaler than do calls of higher pitch. This idea seems to be applicable to song in Mountain Chickadees and Black-capped chickadees.

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SURVIVAL AND LONGEVITY OF THE PUERTO RICAN VIREO

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ABSTRACT.—The Puerto Rican Vireo (*Vireo latimeri*), a Puerto Rican endemic, is declining in at least one forest reserve as the result of pressures from introduced nest predators and an introduced brood parasite. We collected data on adult survival, adult longevity, and juvenile survival from a long-term mist netting study (1973–1999) and a demographic study of color-marked birds (1990–1993) in Guánica Forest, Puerto Rico. Of the adult birds banded in the first three years of the demographic study, 24 of 32 males (75%) and 6 of 7 females (86%) were known to survive until June of the year following their banding. Model-based estimates of adult survival rate from capture/resighting of 65 color-marked birds was 0.74 (± 0.05 SE); for 51 adult males analyzed separately, survival rate was 0.74 (±0.06; data were insufficient to estimate survival rate of females). We recorded a new longevity record for the Puerto Rican Vireo of 13 years, 2 months. Juvenile survival was estimated by enumeration to be 0.40 (±0.15). Juveniles spent prolonged periods on their natal territory, which might increase their probability of surviving to first breeding. Puerto Rican Vireos have relatively high survival rates despite the presence of numerous introduced predators in their habitat, a highly seasonal environment, and the stress of renesting as many as 6 times in a season. *Received 19 Oct. 1998, accepted 25 Feb. 1999.*

Survival rate is an important component of life history models, and it is a central parameter examined in comparative demographic studies (e.g., Ricklefs 1982, Martin 1995). From a conservation perspective, precise estimation of adult and juvenile survival rates is critical because population dynamics often show great sensitivity to variation in these parameters (e.g., Lande 1988, Ryan et al. 1993). Despite their importance, relatively few data are available regarding the survival rates and longevity of tropical birds in general, and insular species in particular (but see Karr et al. 1990, Faaborg and Arendt 1995, Johnston et al. 1997).

The Puerto Rican Vireo (*Vireo latimeri*), is a small (11–12 g) passerine restricted to the island of Puerto Rico (Wetmore 1916). The population of vireos in Guánica Forest, Puerto Rico's largest dry forest reserve, has declined steadily over the past 20 years as a result of parasitism by an exotic avian brood parasite, the Shiny Cowbird (*Molothrus bonariensis*), and nest predation by introduced mammals [rats (*Rattus* spp.), mongoose (*Herpestes auropunctatus*), and feral cats (*Felis catus*); Faaborg et al. 1997; Woodworth 1997, 1999]. A population dynamics analysis indicated that estimates of the Puerto Rican Vireo's population growth rate were very sensitive to adult survival rate; consequently precise estimates of this parameter are crucial for useful population modeling (Woodworth 1999). In this paper we present data on adult and juvenile recoveries, from which we estimate survival rates and longevity of the Puerto Rican Vireo, compare them to temperate mainland congeners, and comment on their implications for persistence of this single-island endemic.

METHODS

We studied the Puerto Rican Vireo population in Guánica Forest Reserve (17° 58′ N, 66° 52′ W) along the southwestern coast of Puerto Rico. The reserve comprises 4,015 ha of mature dry subtropical forest over shallow limestone soils. Rainfall averages 860 mm annually, almost all of which falls between April and November (Murphy and Lugo 1986), and Puerto Rican Vireos generally breed from April through July (Woodworth 1997). Guánica is the site of a long-term constant effort mist netting study of wintering and resident landbirds (see Faaborg and Arendt 1989a), during which 135 Puerto Rican Vireos were marked with aluminum bands from 1973–1996.

From 1990–1993, B.L.W. conducted a demographic study of color-marked vireos in four 50-ha study areas (Woodworth 1997). Resident vireos were captured by playing recorded vireo songs to lure territorial males or pairs into mist nets. Because males were more aggressive than females toward intruders, most known sex birds we captured were males (78%, $n = 65$; 1 bird was of unknown sex). Individuals were resighted by revisiting all territories within the study areas and

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areas within 300 m (about two territory widths) of their borders, and by broadcasting Puerto Rican Vireo song. Color-marked birds were relocated every few days (range: 1–9) throughout the breeding season as part of a study of their seasonal reproductive success (Woodworth 1997). In order to approximate the general assumption of capture-recapture models that all sampling is instantaneous, "capture periods" were defined so as to be short in relation to interval length (breeding season; Smith and Anderson 1987). Thus we defined two sample (capture) periods each breeding season (1990, 1991, and 1993), one consisting of the first two weeks after arrival on the study area, and the second including the two weeks immediately preceding the end of the field season. Birds banded at other times were included only if they were resighted during one of these sampling periods and were treated as if they were originally banded during that sampling period. The June 1992 and January 1993 capture periods consisted of 15 and 11 day visits to the study area, respectively.

We estimated adult survival rate from capture/resighting data on 66 color-marked, territorial adults over 4 years and 7 capture intervals [average interval length = 0.45 ± 0.31 (SE) years]. Five of the birds used in this analysis were originally banded by J.F. and W.J.A. prior to 1990, and so were included in a survival analysis by Faaborg and Arendt (1995), but time periods of the two survival datasets did not overlap. We used the program JOLLY (Pollock et al. 1990) to produce estimates of survival rate under five different capture-recapture models which vary in their assumptions about capture and survival probabilities. These models and their assumptions have been presented in detail elsewhere (Pollock et al. 1990 and references therein). In general, the capture/resighting field methods used here and the more widely used constant effort mist netting methods meet (or not) the assumptions of the Jolly-Seber models to similar degrees, with a few exceptions: (1) although fixed placement of nets in relation to territory boundaries may result in heterogeneous capture probabilities in mistnetting studies (Pollock et al. 1990), we were able to search entire territories for marked individuals; (2) trap response (net shyness) was not a concern in this study because we did not need to catch a bird in a net in order to resight it; (3) we were able to exclude transients from the study (the presence of transients in a sample may bias survival rate estimates if special models are not employed; Pradel et al. 1997); (4) we were able to rule out temporary emigration. Because the capture probability in this study was very high (0.92), we expect the model-based estimators to provide reasonably unbiased estimates of survival rate despite the relatively short time span of the study and moderate sample size (Gilbert 1973).

The program JOLLY provides goodness-of-fit tests to assess the fit of a model to a given data set. Where several models fit the data, likelihood ratio tests were used to test among models, with the simplest adequate model preferred. For statistical comparisons among survival rates we used the χ^2 statistic proposed by Sauer and Williams (1989).

Model-based estimators account for the possibility that a bird is alive and in the study area, but is not resighted in a particular sample period. To facilitate comparison with other studies, we also present survival rate as the number of birds banded in the first three years of the study that were known to be alive in the June following their banding (i.e., enumeration).

Because of the small sample size of fledglings, we could not use model-based estimators of juvenile survival. Thus, juvenile survival was calculated as the proportion of birds originally banded as fledglings that were recaptured or resighted in any subsequent year, and variance was estimated assuming binomial sampling.

As is true in all capture-recapture studies of open populations, dispersal outside of the study area could not be distinguished from mortality. However, typical dispersal rates and distances for the Puerto Rican Vireo are small (Woodworth et al. 1998) so the effect should be relatively minor in this study.

During the demographic study, B.L.W. recaptured 7 birds that had been originally banded prior to 1990. Estimated maximum longevity of the recaptured birds was calculated as the time from initial banding to the last recapture, plus the time from initial banding to the previous June 1, assuming that all birds were hatched on that date (following Klimkiewicz et al. 1983).

RESULTS

We color-banded 51 males, 14 females, 13 fledglings, and 10 birds of unknown sex (winter captures). Of the adult birds banded in the first three years of the study, 24 of 32 males (75%) and 6 of 7 females (86%) were known to survive (i.e., were alive and present on the study area) until the June of the year following their banding (Table 1). Over the four years, there were 59 opportunities for males to survive between breeding seasons, and the males survived in at least 43 of these cases (73%). Females were documented to survive in 11 of 13 opportunities (85%).

Territorial adult Puerto Rican Vireos during this study had an estimated annual survival rate of 0.74 (± 0.05). JOLLY model D, which is based on constant survival and capture probabilites throughout the study, provided the best fit to the data (overall $\chi^2 = 9.7$, df = 8, $P = 0.29$). Our capture/resighting methodology resulted in a very high annual capture probability (0.92 ± 0.03). Male annual survival rate estimated for 51 males was 0.74 (± 0.06; Model D, capture probability = 0.95 ± 0.02). Data for 14 females were insufficient to fit a model describing female survival because most were banded in the last year of the study. Juvenile

TABLE 1. Bandings and resightings of male Puerto Rican Vireos known to be at least one year old when banded (demographic study only). The 8 sample periods, each 2 weeks long, took place in April 1990, July 1990, March 1991, August 1991, June 1992, January 1993, March 1993, and August 1993, resulting in 7 intervals. No new birds were banded during sample periods in July 1990, June 1992, or August 1993.

Sample period when banded	Number banded	Returns in sample period following banding						
		One	Two	Three	Four	Five	Six	Seven
Apr 1990	10	8	7	7	4	2	1	1
Mar 1991	7	5	6	5	6	6	—	—
Aug 1991	13	10	11	8	6	—	—	—
Jan 1993	3	3	2	—	—	—	—	—
Mar 1993	18	17	—	—	—	—	—	—
Total	51	43	26	20	16	8	1	1

survival rate from fledging to first breeding was estimated at 0.40 (± 0.15; $n = 10$).

The oldest Puerto Rican Vireo we recaptured was at least 13 years, 2 months (13-02) old, exceeding the previous longevity record for the Puerto Rican Vireo by nearly 4 years (09-04; Faaborg and Arendt 1989b). Three other birds that nearly matched the previous record were also recaptured (09-01, 09-02, and 09-02). All were color-banded territorial males that we observed over 1–2 complete breeding seasons before they disappeared or the study ended. None had dispersed more than 500 m in the decade since they were originally banded (see Woodworth et al. 1998 for details of dispersal behavior).

DISCUSSION

Faaborg and Arendt (1995) estimated an adult annual survival rate of 0.68 (± 0.08) for the Puerto Rican Vireo population in Guánica, based on their long-term mist netting study (Jolly-Seber model D, 19 individuals over 18 years and 15 capture intervals). Although their mean survival value is slightly less than that presented here (probably because of the inclusion of a higher proportion of female birds, along with non-territorial individuals), the two estimates are not significantly different ($\chi^2 = 0.40$, df = 1, $P > 0.05$).

Our Puerto Rican Vireo survival rate estimate is high relative to survival and recovery rates reported for temperate vireos. Recovery percentages of White-eyed Vireos (*Vireo griseus*) studied over 9 years on their breeding grounds were 48% for males, and 50% for females (Hopp et al. 1999). Return rates of adult male Black-capped Vireos (*V. atricapillus*) to breeding territories in central Texas were 55–75% (Grzybowski 1991). The survival rate of Red-eyed Vireos (*V. olivaceous*) based on returns to breeding grounds in Maryland, was estimated at 59% (Jolly-Seber model A; Nichols et al. 1981). Return rates of adult Gray Vireos (*V. vicinior*) to wintering territories in Mexico were 46–71% (Bates 1992), and for Bell's Vireo (*V. bellii*) returning to breeding territories in California, 47% (Salata 1983). Interestingly, compared to survival rate estimates for other tropical island passerines studied to date, the survival rate of the Puerto Rican Vireo is not unusually high [e.g., average 68% (51–79%) for 7 Puerto Rican species, Faaborg and Arendt 1995; 65.3% (45–85%) for 17 Trinidadian species, Johnston et al. 1997; and 76% (55–88%) for 5 Hawaiian species, van Riper 1987, Lepson and Freed 1995, Ralph and Fancy 1995, Woodworth et al. in press].

Likewise, the longevity record for the Puerto Rican Vireo of 13 years, 2 months is long relative to most of its temperate congeners. Records for six other temperate *Vireo* species range from 6 years, 1 month to 10 years (Davis 1995, Kennard 1975, Klimkiewicz et al. 1983, Rodewald and James 1996). The record for the Warbling Vireo (*Vireo gilvis*), a neotropical migrant, is very similar (13-01, Klimkiewicz et al. 1983) to the Puerto Rican Vireo. Such records are complicated by many factors (Krementz et al. 1989). Although it is surprising that such a seemingly long longevity record from a nonmigratory species would be equaled by a long distance migrant, it is worth noting that over 15,000 Warbling Vireos have been banded (Klimkiewicz et al. 1983), but only a few hundred

Puerto Rican Vireos have been banded and many of these have been long lived.

The relatively high survival and longevity of this insular species is remarkable in light of the presence of numerous introduced predators in its habitat, high rates of nest failure causing females to renest up to 6 times in a season (Woodworth 1997), and the stresses of a highly seasonal environment (almost no rain falls from December to March, and Guánica loses up to 50% of its leaf area in winter; Murphy and Lugo 1986). Puerto Rican Vireos have a small clutch size relative to temperate vireos (Woodworth 1995), which, when coupled with the generally observed trade-off between fecundity and survival (Martin 1995), might allow birds to survive through more breeding seasons (Cody 1966). In addition, a non-migratory insular species might outlive its migratory counterparts because it does not pay the price of annual migration.

Juvenile survival rates of passerines are poorly known, especially for tropical birds. Return rates of juvenile Bell's Vireos and Black-capped Vireos were measured as 24%, although actual survival rate is likely to be higher (Salata 1983, Grzybowski 1991; respectively). Survival of juvenile Wood Thrush (*Hylocichla mustelina*) in their first 12 weeks is only 0.42 (Anders et al. 1997). Juvenile survival may be enhanced if young are allowed to remain in their natal territory for an extended period (discussed in Karr et al. 1990) as Puerto Rican Vireo fledglings have been observed to do (at least 80–98 days post-fledging; Woodworth 1995).

A population dynamics model of this population showed that, as is common in many population models, the vireo's predicted population growth rate was greatly dependent upon the value of adult survivorship used in the model (Woodworth 1999). Therefore, a precise and accurate estimate of adult survivorship is critical to evaluating the long-term prospects for survival of this population. The close agreement between two independent estimates (Faaborg and Arendt 1995 and this study) of adult survival rate for this population improves confidence in the predictions of a model using these estimates, although additional data on female and juvenile survivorship is needed.

The relatively high adult and juvenile survival rates we documented would seem to bode well for the persistence of Puerto Rican Vireos in Guánica Forest. However, other work on this population has shown that the vireos suffer extremely high nest losses to native and introduced predators, and to parasitism by the exotic Shiny Cowbird (Woodworth 1997). Despite as many as 6 nest attempts in a single season, females succeed in fledging young from only 0.41–0.67 nests per year (Woodworth 1997). These factors result in an overall negative population growth rate for the vireo over the range of "reasonable" survival rate values (the 95% confidence limits of the estimates; Woodworth 1999). Thus, the declines observed over the previous decade (Faaborg et al. 1997) are likely to continue unless active management is undertaken to reduce predation and/or brood parasitism in the forest.

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EFFECTS OF PRIOR RESIDENCE AND AGE ON BREEDING PERFORMANCE IN YELLOW WARBLERS

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ABSTRACT.—Age-related increases in reproductive success could be the result of better survival by successful breeders (survival hypothesis), greater dispersal by unsuccessful breeders (dispersal hypothesis), and/or age-related differences in the ability to compete for breeding opportunities (constraint hypothesis). We used banding and nesting data from four consecutive breeding seasons to examine the effects of prior residency on several indices of breeding performance in Yellow Warblers (*Dendroica petechia*). We compared the breeding performance of returning birds with that of new arrivals, and of individuals between successive breeding seasons. There were no differences in clutch size between new arrivals and returning individuals, nor within individuals between successive breeding seasons. Among males, prior residence had no effect on whether a clutch was started, but among females the number of prior residents that initiated a clutch was higher than expected, and the number of new arrivals that did not was lower than expected. In contrast, there were no differences in laying or hatching date between new arrivals and returning individuals, but within-individual comparisons showed that males bred earlier in successive breeding seasons. Previous reproduction increased subsequent return rates only 1 out of 3 years in both sexes. Returning males were larger than new arrivals, but there were no differences in females. Within-individual size increases between successive breeding seasons occurred in both sexes. These results are consistent with the constraint hypothesis, but the proximate mechanisms by which these differences arise remain to be determined. *Received 1 Oct. 1998, accepted 20 Feb. 1999.*

Age-related increases in reproductive success have been documented in many bird species (reviewed by Sæther 1990, Forslund and Pärt 1995). Several hypotheses have been proposed to explain this phenomenon. Forslund and Pärt (1995) divided these hypotheses into three groups depending on whether they are based on (1) the gradual appearance or disappearance of certain phenotypes, (2) the lifetime optimization of reproductive effort, or (3) age-related improvements in competence. These three groups of hypotheses are not mutually exclusive.

In the first group of hypotheses, differences in reproductive success among age classes are not viewed as the result of individuals increasing their reproductive success with age, but rather as a result of the elimination of some phenotypes from the population. The probability of breeding may be positively correlated with the likelihood of survival (survival hypothesis) or negatively correlated with the likelihood of dispersal (dispersal hypothesis; e.g., Smith 1981, Nol and Smith 1987, Wheelwright and Schultz 1994); either mechanism would yield a positive correlation of age with reproductive success. These hypotheses are clearly not applicable to species that show within-individual increases in reproductive success between successive reproductive bouts (Pyle et al. 1991, Smith 1993).

The second group of hypotheses asserts that older individuals allocate more effort to reproduction. The restraint hypothesis states that this is because residual reproductive value decreases with age, so as individuals become older the value of current reproduction increases relative to the value of future reproduction. This idea is based on the theoretical trade-off between current and future reproduction (Williams 1966, Pianka and Parker 1975) and only applies if the probability of survival decreases with age. Reproductive effort may also increase with age if age-specific improvements in breeding experience make each successive reproductive bout relatively less expensive (Reid 1988). Accordingly, individuals may allocate the same relative effort into reproduction as they age, but increase it in absolute terms. These hypotheses are based on life history, in which age is the explanation.

In contrast, hypotheses in the third group, collectively known as the constraint hypothesis (Curio 1983), are based on ecological considerations. These hypotheses posit that younger individuals are unable to reproduce

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as well as older ones because the former are less capable of competing for breeding opportunities. Age-related variance in reproductive success is considered to be a result of differences in the ability to obtain territories, forage efficiently, resist competitors, avoid predators, attract prospective mates, and/or raise offspring. These factors may, in turn, be affected by the familiarity of individuals with the breeding area. This effect, known as "local experience" or "local familiarity", may allow prior residents to exploit the resources of an area more efficiently than new arrivals (Hinde 1956, Greenwood 1980).

Here we used banding and nesting data from four consecutive breeding seasons to examine the effects of prior residency on several indices of breeding performance in Yellow Warblers (*Dendroica petechia*). The Yellow Warbler is a socially monogamous 10 g passerine found from Alaska and northern Canada to the coasts of Peru and Venezuela, including the Caribbean and Galapagos islands. Formerly, several species, or subspecies were recognized (Aldrich 1942, Bent 1963), but currently these are considered "groups" of one species (Sibley and Monroe 1990). Southern, non-migratory subspecies are easily distinguished from North American migratory populations by morphological differences (Aldrich 1942, Wiedenfeld 1991, Curson et al. 1994) and by phylogenetic analyses based on mitochondrial DNA (Klein and Brown 1994). The migratory group (*Dendroica petechia aestiva*) used in this study, breeds in the United States and Canada and winters in Central America, northern South America, and the Caribbean.

Using morphological and nesting data from four consecutive breeding seasons, we first determined whether prior residence increased the likelihood or timing of breeding in Yellow Warblers. We then tested the survival and dispersal hypotheses by examining whether individuals were more likely to breed or to do so earlier in successive seasons, and we dealt with the possible disappearance of phenotypes from the population by relating morphology and breeding performance to subsequent return rates. Finally, we explored morphological differences between new arrivals and returning birds, and individual morphological changes between successive breeding seasons.

METHODS

Data were collected from 1992 to 1995 at a 5 ha (approximately 500 m × 100 m) area between Pointe à Fourneau and Pointe du Moulin on Île Perrot, Quebec, Canada (45° 22′ N, 73° 51′ W). Yellow Warblers began arriving to our study area during the second week of May in all four years. Typically one or two males arrived first; two or three days later large numbers of males arrived, along with the first females. Nests are built exclusively by females, and nest-building takes about four days. Eggs are usually laid on consecutive days, at a rate of one per day. Clutches normally contain four or five eggs. Incubation begins when the last egg is laid, and the first egg hatches 10 days later. During the nestling period only females brood, but both parents feed their nestlings. Fledging normally occurrs approximately 10 days after hatching.

Adult birds were captured using mist nets; each bird captured was banded with a U.S. Fish and Wildlife Service (USFWS) aluminum band and three colored plastic bands. Mist nets were operated throughout the study area on a daily basis from May to early June, starting at dawn and ending at 11:00–13:00, weather-permitting. Three to five nets were used simultaneously in close proximity to one another, and these were moved such that the entire study area was sampled every 7–10 days. After 3 or 4 such cycles, we focused our effort for 1–2 weeks on unbanded birds whose nests had already been found. Nestlings were banded at the nest when they were six days old, but only with a USFWS band. In any given year, each adult bird captured was classified as a returning bird if it had been banded as an adult in previous years; otherwise it was classified as a new arrival. It is impossible to know with certainty whether every bird was captured every year, so a few returning birds may have been misclassified as being new to the site; all tests must therefore be considered conservative.

Several standard morphological measurements were taken from each bird: the lengths of the flattened wing chord, the ninth primary feather, the outermost rectrix, and the tarsus. The weight of each bird was recorded to the nearest 0.1 g using a calibrated Pesola® spring balance.

From early May to the middle of June the area was thoroughly searched daily for nests, concentrating in areas where birds had been banded and using behavioral cues from females. Except during days of continuous rain, every nest was visited daily to document the chronology of nest building and egg laying. Many nests failed as a result of harsh weather or predators; renesting attempts usually followed. Two categorical measures were used to determine the breeding stage reached: whether at least one egg was laid at a given nest (clutch initiation) and whether at least one egg hatched. Clutch initiation and hatching dates were used to indicate the timing of reproduction; replacement nests were not used in these comparisons. Laying date was defined as the date the first egg was laid, and

TABLE 1. Frequency of Yellow Warblers that reached the "first egg" stage depending on whether they were new to the area or returning birds, by year and sex (expected frequencies in parentheses). Heterogeneity tests: males: $\chi^2 = 0.006$, df = 2, $P > 0.05$; females: $\chi^2 = 0.706$, df = 2, $P > 0.05$.

		Did not reach the "first egg" stage		Reached the "first egg" stage			
	n	New	Return	New	Return	χ^2	*P*
Males							
1993	47	13 (13.3)	13 (12.7)	11 (10.7)	10 (10.3)	0.02	≫0.05
1994	71	30 (31.1)	15 (13.9)	19 (17.9)	7 (8.1)	0.09	≫0.05
1995	53	19 (19.3)	12 (11.7)	14 (13.7)	8 (8.3)	0.01	≫0.05
Total	171	62 (63.2)	40 (38.8)	44 (42.8)	25 (26.4)	0.06	≫0.05
Females							
1993	46	21 (16)	2 (7)	11 (16)	12 (7)	8.32	0.004
1994	66	23 (21.1)	8 (9.9)	22 (23.9)	13 (11.1)	0.52	≫0.05
1995	45	15 (11.4)	4 (7.6)	12 (15.6)	14 (10.4)	3.65	0.056
Total	157	59 (48.3)	14 (24.7)	45 (55.6)	39 (28.3)	11.8	0.001

similarly, hatching date as the date the first egg hatched. As used here, the terms "clutch initiation", "first-egg stage", "laying date", and "hatching date" refer to features of the nest, and therefore apply to both the male and the female associated with the nest. In several other species clutch size often decreases as the breeding season progresses (Erikstad et al. 1985, Murphy 1986, Perrins and McCleery 1989), so only initial nesting attempts were used in comparisons of clutch size. Other estimates of breeding performance were not used in these analyses because intrusive experiments, beginning at the time of hatching but random with respect to the variables examined here, were carried out every year (Lozano and Lemon 1995, 1996, 1998).

Although the date on which birds began to arrive during the four years of the study varied by up to two weeks, the first day on which an egg was laid in the population was fairly consistent. From 1992 to 1995, these first egg dates were May 26 and 24, June 2, and May 25 respectively. These yearly first egg dates were used to account for variation in laying date among years; relative laying and hatching dates of individual nests are defined as the number of days after the respective yearly first egg dates, added to the mean first egg date from all four years.

Relationships between categorical variables were examined using Fisher's exact tests for $n < 20$, χ^2 tests for $40 \geq n > 20$, and χ^2 with Yates' adjustment for continuity for $n > 40$ (Cochran 1954, Fienberg 1980, Everitt 1992). Because the mobility of the two sexes may have differed, especially early in the breeding season when the birds were banded, the data were analyzed separately for males and females. Within-individual increases in size and breeding performace between consecutive seasons were tested with one-tailed paired *t*-tests or Wilcoxon matched-pairs signed ranks tests; if an individual was sampled repeatedly in several years, data from only the first 2 years were used in these analyses. Size differences between groups were also assessed using the four morphological variables in a MANOVA, with group and year as the independent variables. All statistical analyses were performed or verified using Statistica (5.1 and 98, under Windows 3.11 and 95). Statistical significance was accepted at $P < 0.05$.

RESULTS

Among males there was no relation between prior residence and whether a clutch was initiated in their nests (Table 1). In contrast, among females the number of prior residents that initiated a clutch was higher than expected, as was the number of birds new to the area that failed to initiate a clutch. The pattern was the same in all three years, significant in 2 of the 3 years and in the analysis with data pooled from all years (Table 1). Finally, there were no significant differences in first egg date ($F_{1,151} = 0.65$, $P > 0.05$), clutch size ($F_{1,147} = 0.17$, $P > 0.05$), or hatching date ($F_{1,110} = 0.21$, $P > 0.05$) between birds new to the area and returning individuals.

Differences between groups do not necessarily imply changes within individuals. Comparisons within individuals in successive breeding seasons show no increases in clutch size in either sex (Wilcoxon matched-pairs signed-ranks tests: males $Z = 0.36$, $n = 18$, $P > 0.05$; females $Z = 0.82$, $n = 21$, $P > 0.05$). However, for males laying date was significantly earlier in successive breeding seasons, on average 2.8 days earlier (Wilcoxon matched-pairs signed-ranks test: $Z = 1.78$, $n = 18$, $P = 0.04$; Fig. 1a). This was largely due to late-nesting males nesting markedly earlier in the following year, as there was little difference among males that nested in late

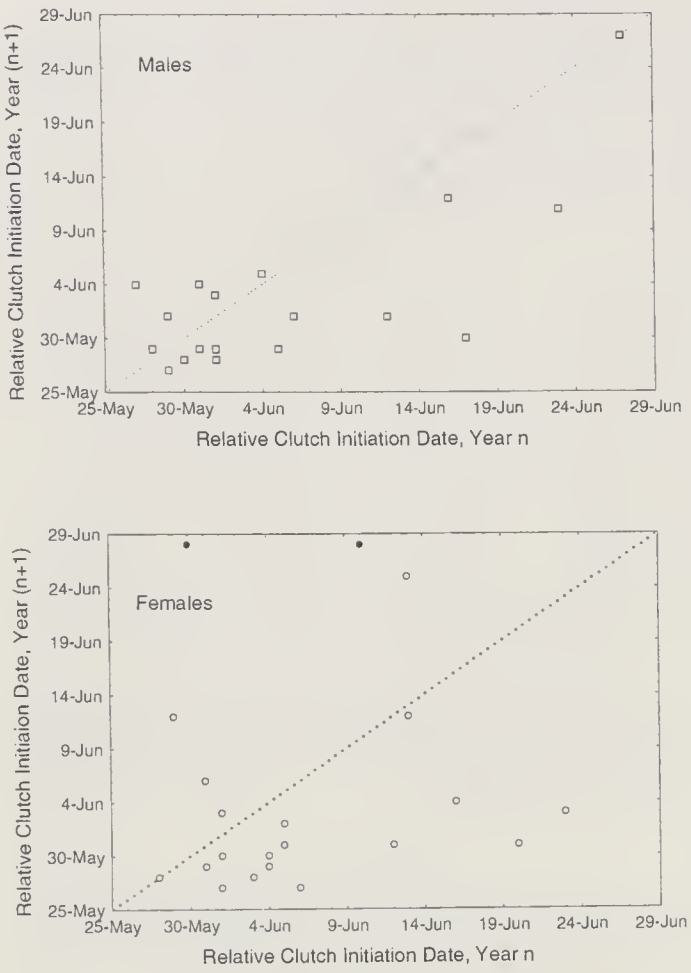

FIG. 1. Clutch initiation dates by individuals in consecutive breeding seasons, corrected for differences between years (see methods). The dashed lines have a slope of 1, which would result if clutch initiation occurred on the same relative date in successive breeding seasons. The two solid circles in the lower graph were categorized as outliers (see results).

May–early June (Fig. 1a). In contrast, the difference in females was only 1.3 days earlier, and was not significant (Wilcoxon matched-pairs signed-ranks test $Z = 0.93$, $n = 21$, $P = 0.18$; Fig. 1b). However, the relationship is heavily influenced by 2 nests that may have been re-nesting attempts. Without these outliers the margin becomes 4.0 days earlier and statistically significant (Wilcoxon matched-pairs signed-ranks test: $Z = 1.85$, $n = 19$, $P = 0.032$; Fig. 1b). The removal of these outliers did not lead to categorically different conclusions in all other analyses.

A significant relationship between breeding performance and subsequent return occurred in only one of the three years. Both males and females that had at least started a clutch in 1992 were more likely to return the following year (Table 2), but there was no evidence of this relationship in the other 2 years. Although the results were also significant when using pooled data, this was due solely to the 1992 results (Heterogeneity χ^2 tests: males $P = 0.014$; females $P = 0.065$; Table 2). Similar results were obtained if return frequency was compared to having hatched at least one offspring. Among birds that nested, there were no significant differences in first egg date ($F_{1,166} = 0.60$, $P > 0.05$), clutch size ($F_{1,166} = 0.21$, $P > 0.05$), or hatching date ($F_{1,137} = 1.10$, $P > 0.05$) between birds that subsequently returned and those that did not. Therefore, the effect of breeding performance on subsequent return, as measured here, was certainly not consistent, if present at all.

TABLE 2. Relationship between having reached the "first egg" stage in one breeding season and returning in the following year. Continuity adjusted χ^2 or Fisher's exact tests (*) were used depending on the sample size and its distribution (expected frequencies in parentheses). Heterogeneity tests: males: $\chi^2 = 8.51$, df = 2, $P = 0.014$; females: $\chi^2 = 5.461$, df = 2, $P = 0.065$.

		Did not reach the "first egg" stage		Reached the "first egg" stage			
	n	Did not return	Returned	Did not return	Returned	χ^2	*P*
Males							
1992	67	29 (20.5)	3 (11.7)	14 (22.5)	21 (12.5)	16.5	<0.001
1993	47	15 (14.9)	11 (11.1)	12 (12.1)	9 (8.9)	0.07	≫0.05
1994	71	33 (32.3)	12 (12.7)	18 (18.7)	8 (7.3)	0.01	≫0.05
Total	185	77 (67.4)	26 (35.6)	44 (53.6)	38 (28.4)	8.07	0.005
Females							
1992	37	8 (4.1)	1 (4.9)	9 (12.9)	19 (15.1)	*	0.005
1993	46	17 (14.5)	6 (8.5)	12 (14.5)	11 (8.5)	1.49	≫0.05
1994	66	25 (26.3)	6 (4.7)	31 (29.7)	4 (5.3)	0.31	≫0.05
Total	149	50 (43.1)	13 (19.9)	52 (58.9)	34 (27.1)	5.17	0.023

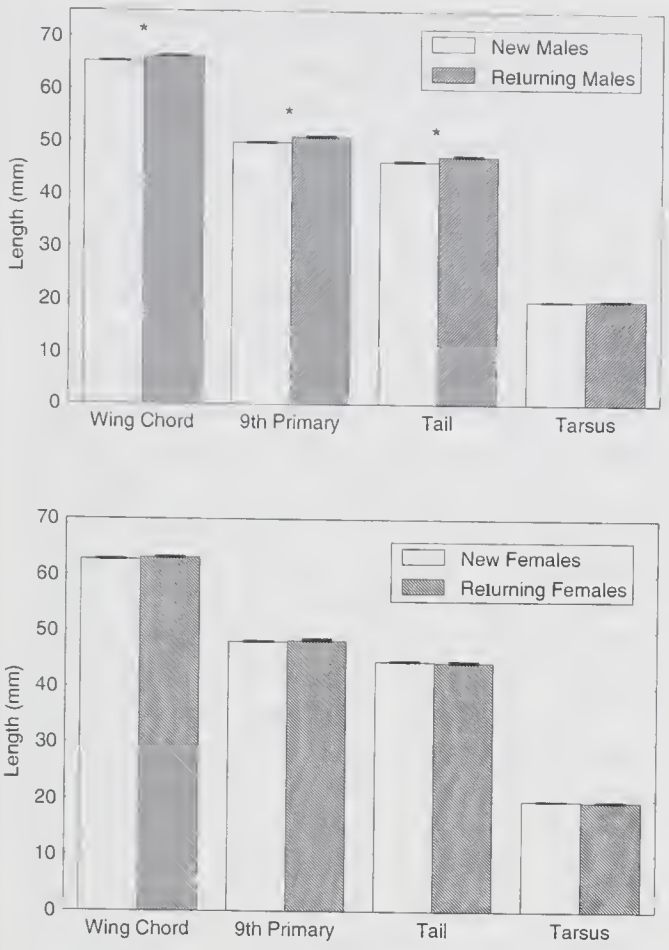

FIG. 2. Mean size (+SE) of Yellow Warblers versus residency history. MANOVAs were carried out using all variables (Males: Wilks' $\lambda = 0.901$, $F_{4,151} = 4.14$, $P = 0.003$; Females: Wilks' $\lambda = 0.976$, $F_{4,133} = 0.803$, $P \gg 0.05$). Asterisks indicate significant differences ($P < 0.05$) resulting from univariate ANOVAs.

Returning males were significantly larger than new arrivals (Wilks' $\lambda = 0.901$, $F_{4,151} = 4.14$, $P = 0.003$; Fig. 2) but returning females were not larger than new arrivals (Wilks' $\lambda = 0.976$, $F_{4,133} = 0.803$, $P > 0.05$; Fig. 2). In contrast, there were significant within-individual increases in size between successive breeding seasons in both sexes (Table 3).

Finally, there were no significant differences in morphology between nesting birds that subsequently returned and nesting birds that did not return, in either sex (MANOVA: Males Wilks' $\lambda = 0.989$, $F_{4,167} = 0.448$, $P > 0.05$; Females Wilks' $\lambda = 0.9477$, $F_{4,125} = 1.724$, $P > 0.05$).

DISCUSSION

The effects of prior residency on breeding performance differed substantially between the sexes. Comparisons of new arrivals with returning birds showed that the likelihood of breeding increased with prior residency in females, but not in males. Among birds that nested, there were no significant differences in the timing of breeding and clutch size between new arrivals and returning birds. However, within-individual comparisons showed that males began breeding significantly earlier in subsequent breeding seasons. Therefore, the effect of prior residency was greater for females than for males; in females local experience affected the prospect of breeding, and in males it only affected the timing of breeding.

There can be several advantages to breeding earlier. Early breeders often have larger clutches (Erikstad et al. 1985, Murphy 1986, Perrins and McCleery 1989). In the population we studied the median clutch size decreased from five eggs in nests started before June 15, to four eggs in nests initiated thereafter. Fledglings from earlier nests also have

TABLE 3. Within-individual increases in size between successive breeding seasons in Yellow Warblers and results from one-tailed paired *t*-tests.

Variable	*n*	Difference (mm) $Year_{x+1} - Year_x$	SE	*t*	*P*
Males					
Tail	48	0.50	0.32	1.55	0.06
Wing chord	49	0.46	0.21	2.14	0.02
Ninth primary	49	0.97	0.28	3.53	<0.001
Tarsus	49	0.20	0.14	1.49	0.07
Females					
Tail	31	0.27	0.31	0.89	>0.05
Wing chord	31	0.74	0.34	2.18	0.02
Ninth primary	31	0.74	0.32	2.32	0.01
Tarsus	31	0.31	0.14	2.28	0.02

more time to develop before migration, which in our area begins in the latter half of July. Perhaps most important, nest losses, whether they are due to inclement weather or predation, are very common in open nesting birds (Nice 1957, Martin and Li 1992). An earlier start provides a longer available breeding season, which enhances the probability of renesting following nest losses (Lozano et al. 1996).

Birds that arrive first may also benefit by obtaining preferred territories (Wooller and Coulson 1977, Newton 1988, Morris and Lemon 1989, Lemon et al. 1996). On the other hand, early arrivals also risk death from exposure to cold weather and lack of food early in the spring (Anderson 1965, Whitmore et al. 1977). Several other researchers have shown that earlier arrivals are larger and in better condition than later arrivals (e.g., Arvidsson and Neergaard 1991, Lozano 1994, Stolt and Fransson 1995). Size is important because arrival time depends partially on the ability to withstand adverse conditions early in the breeding season. In our population, however, it is unlikely that size affected arrival time, because there was little variance in arrival dates, but even given similar arrival times, large size may still be advantageous in intrasexual competition during territory establishment and defense (Arcese 1987, Hogstad 1989).

Individual males were larger in subsequent breeding seasons, and, as a group, returning males were also larger than males new to the area. In contrast, returning females were not significantly larger than females new to the area, but individual females recaptured in consecutive breeding seasons were larger from one breeding season to the next. At first glance, the latter results may appear contradictory, but the two analyses are not equivalent. Females may increase in size between consecutive breeding seasons without necessarily leading to returning females being larger than new arrivals. The differences between the sexes may result, for instance, if the breeding dispersal or size variance of females is greater than that of males.

Size may also play a role in mate choice later in the season. In Yellow Warblers extrapair paternity is widespread (Yezerinac et al. 1995), and within-pair paternity increases with male size (Yezerinac and Weatherhead 1997). Female preference for larger males may occur if size is an honest indicator of phenotypic or genotypic quality, or if size is being used as an indicator of age. If there is a genetic component of survival ability, age, in itself, would be a measure of genetic quality, and females would benefit by mating with older males (Manning 1985).

We do not know the exact ages of all adult birds studied, but we assume the mean age of new arrivals is less than that of returning birds. This is because in Yellow Warblers breeding dispersal is limited (Yezerinac and Weatherhead 1997), but natal dispersal is common, as it is in birds in general (Greenwood 1980, Greenwood and Harvey 1982, Clarke et al. 1997). We have no measures of dispersal exclusive of mortality, but only 4.5% of all nestlings returned, compared to an overall yearly return of 36% for adults. Although we cannot be certain that every individual classified as a new arrival was only one year old, returning birds were, by necessity, at least two years old. Therefore, when compared as two separate groups, not as individuals, it is safe to conclude that returning birds were older than new arrivals (see also Yezerinac and Weatherhead 1997).

Age-dependent increases in reproductive success have been well documented in birds (reviewed by Sæther 1990, Forslund and Pärt 1995), but the proximate mechanisms responsible have been difficult to determine because potential factors are often correlated. Apparent age-dependent increases in reproductive success can be a statistical consequence of the gradual disappearance of poor breeders from a population, which would result if the phenotypic or genotypic quality of an individual affects both its chances of breeding and surviving (Curio 1983). Alternatively, individuals may be more likely to disperse to other areas in subsequent breeding seasons after a failed breeding attempt (Harvey et al. 1979, Bensch and Hasselquist 1991). Either mechanism would yield a difference in reproductive success between age classes, but this did not occur in our study. Except for one year, breeding performance did not affect subsequent return for either sex. Furthermore, there were no morphological differences between birds that subsequently returned and those that did not.

These results also confirm that non-breeders were not actually transients, captured while on route to their final destinations. Had this been the case they would have been less likely to return than breeders.

The restraint hypothesis proposes that young individuals deliberately withhold reproductive effort. Life-history theory suggests that age of first reproduction is an important component of lifetime reproductive success (Charlesworth 1980, Clutton-Brock 1988). Our records show that 64% of all adult Yellow Warblers fail to return, which makes it very unlikely that individuals would purposely forego the opportunity to reproduce, especially after having already migrated to the breeding grounds. Moreover, the decision not to reproduce would be optimal only if there is a large cost to reproduction, but we found that breeding was not related to subsequent return rates. Therefore, the restraint hypothesis is probably not appropriate to explain age-dependent increases in reproductive success in Yellow Warblers or other short-lived migratory species (Wheelwright and Schultz 1994).

Our results are consistent with the constraint hypothesis, which predicts that younger birds are disadvantaged when competing for breeding opportunities. However, it is difficult to know to what extent these results are caused by differences in local experience or by age in itself. Experimental work will be required to determine the ecological and proximate mechanisms responsible for these differences (Martin 1995).

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DISTRIBUTION AND HABITAT ASSOCIATIONS OF THREE ENDEMIC GRASSLAND SONGBIRDS IN SOUTHERN SASKATCHEWAN

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ABSTRACT.—We conducted 1675 point counts on 93 survey routes to determine the distribution and habitat associations of three endemic grassland songbirds across the four prairie ecoregions of southern Saskatchewan, Canada. Within the four habitat types surveyed, Sprague's Pipits (*Anthus spragueii*) and Chestnut-collared Longspurs (*Calcarius ornatus*) occurred more frequently in native and seeded pastures than in hayland and cropland, whereas Baird's Sparrows (*Ammodramus bairdii*) occurred as frequently in hayland as in native and seeded pastures. The occurrence of Baird's Sparrows and Chestnut-collared Longspurs did not differ significantly between lightly, moderately, and heavily grazed native pastures, whereas Sprague's Pipits occurred less frequently in heavily grazed pastures. Sprague's Pipits and Chestnut-collared Longspurs occurred more often in the drier prairies of the southern portion of the province, but Chestnut-collared Longspurs were virtually absent from the cypress upland ecoregion. In contrast, Baird's Sparrows occurred most frequently in the semi-arid grasslands of the moist-mixed grassland ecoregion. In native pastures, Chestnut-collared Longspurs were associated with a lower density of short grasses and lesser amounts of litter whereas Baird's Sparrows were associated with a higher density of taller grasses and sparse shrub cover. Our results suggest that conservation programs that convert annually tilled cropland to perennial forage could provide additional habitat for endemic grassland birds.
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Land settlement and agriculture have greatly altered the landscape of southern Saskatchewan. Only 17% of the province's original native prairie remains (Samson and Knopf 1994) and is currently threatened by cultivation, over-grazing by livestock, invasion by exotic plant species, and urban development. In areas of Saskatchewan where soils and landscapes are particularly suited for crop production, less than 0.1% of the original native prairie remains (Riemer et al. 1997).

Despite the loss of native grassland, Saskatchewan supports a diverse grassland avifauna (Smith 1996), including 11 of the 12 primary endemic, and 17 of the 25 secondary endemic grassland bird species as outlined by Knopf (1994). Primary endemic species generally have more restricted breeding ranges (Sauer et al. 1997) and are less flexible in their habitat requirements than more broadly distributed species (Owens and Myres 1973, Knopf 1996, Davis and Duncan in press). Consequently, continental populations of 7 of the 11 primary endemic species are currently in decline (Sauer et al. 1997), possibly as a result of loss and degradation of native prairie habitat.

Information on the habitat associations of endemic songbirds can provide insight into population declines by identifying habitat features that correlate with their occurrence. This information may be used in making management decisions and formulating land-use policies. Although many researchers have examined habitat selection by grassland songbirds (Cody 1968, Owens and Myres 1973, Whitmore 1979, Rotenberry and Wiens 1980, Johnson and Temple 1986, Mahon 1995), little research has been focused on birds of the northern mixed-grass prairie. Furthermore, most studies in the mixed-grass prairie region have been conducted on intensively managed sites (Dale 1983, Winter 1994, Madden 1996, Dale et al. 1997) or were located within a small geographic area (Arnold and Higgins 1986, Sutter 1996; but see Johnson and Schwartz 1993, Davis and Duncan in press).

We examined habitat associations and the distribution of three endemic songbird species of the northern mixed-grass prairie across the entire Prairie Ecozone of southern Saskatchewan. The objectives of the study were (1) to determine whether the frequencies of occur-

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rence of Sprague's Pipit (*Anthus spragueii*), Baird's Sparrow (*Ammodramus bairdii*), and Chestnut-collared Longspur (*Calcarius ornatus*) differ among native pasture, seeded pasture, hayland, and cropland; (2) to determine whether various levels of grazing intensity influence the occurrence of these species; (3) to determine the distribution of the three species relative to the prairie ecoregions of Saskatchewan; and (4) to identify structural components of native prairie vegetation important in predicting songbird occurrence.

STUDY AREA AND METHODS

Study area.—We conducted grassland bird surveys throughout the Prairie Ecozone of southern Saskatchewan. The Prairie Ecozone covers 24,103,000 ha and comprises four ecoregions: cypress upland, mixed grassland, moist-mixed grassland, and aspen parkland (Fig. 1; Ecological Stratification Working Group 1995). The cypress upland in the extreme southwestern portion of the province rises 400–500 m above the prairie landscape. This region is characterized by sloping escarpments, valleys, and coulees. Wheatgrass (*Agropyron* spp.) and speargrass (*Stipa* spp.) dominate the dark brown soils of the lower elevations, whereas fescue (*Festuca* spp.) prairie predominates on the slopes and at higher elevations. The mixed grassland is the driest region of Saskatchewan and is characterized by wheatgrass, speargrass, and blue grama grass (*Bouteloua gracilis*). Because of the lack of moisture, trees and wetlands are scarce; shrubs are restricted to mesic areas. The moist-mixed grassland represents the northern extent of the open grasslands in Saskatchewan. This region is characterized by semiarid conditions and dark brown soils. Speargrass, wheatgrass, and deciduous shrubs predominate. The aspen parkland ecoregion is characterized by trembling aspen (*Populus tremuloides*) groves and fescue grasslands, although the latter habitat is now rare (Sask. Wetland Conserv. Corp., unpubl. data).

Bird surveys were conducted in native pasture, seeded pasture, hayland, and cropland. Survey routes were designed to sample mostly grassland habitat, although each of the four habitat types was sampled on most routes. Native prairie was characterized by *Stipa* spp., June grass (*Koeleria cristata*), northern wheatgrass (*Agropyron dasystachyum*), western wheatgrass (*A. smithii*), blue grama grass, *Carex* spp., club moss (*Selaginella densa*), pasture sage (*Artemisia frigida*), and various forbs. The most common shrubs were western snowberry (*Symphoricarpos occidentalis*), rose (*Rosa* spp.), and wolf willow (*Elaeagnus commutata*). Seeded pasture was defined as land that had been broken and seeded with exotic perennial grasses for grazing, most commonly crested wheatgrass (*Agropyron cristatum*) or brome grass (*Bromus* spp.), with alfalfa (*Medicago* spp.) or sweet clover (*Melilotus* spp.) sometimes present. Hayland was defined as cultivated land that had been seeded to perennial crops for haying. Vegetation on hayland ranged from 100% alfalfa, to mixes of alfalfa, sweet clover and introduced grasses such as brome grass, crested wheatgrass, or bluegrass (*Poa* spp.). Cropland was cultivated land that was seeded to annual crops, most commonly wheat (*Triticum aestivum*) or canola (*Brassica* spp.).

Route selection.—We numbered (1–42) townships from the U.S. border to the northern extent of the aspen parkland, and renumbered (1–64) range locations from the Manitoba border west to the Alberta border. The starting points of 76 routes were then located by selecting township-range numbers from a random number table. Because the target species (Baird's Sparrow) was believed to be a grassland specialist (Cartwright et al. 1937, Owens and Myres 1973), we only included townships where most point counts (≥80%) could be located in grassland habitat. Thus more routes were established in the mixed grassland ecoregion than the other ecoregions because most of the grassland in Saskatchewan exists in this region (Saskatchewan Digital Land Cover Project, unpubl. data). Because Baird's Sparrow was a threatened species in 1994 (Goossen et al. 1993), we assumed they were uncommon and established an additional 19 non-random routes in areas where the species was thought to occur regularly. The proportion of point counts in grassland habitat was nearly identical for random and non-random routes (79 and 80%, respectively).

Bird occurrence.—Six surveyors recorded the number of singing males using five-minute, 100-m fixed radius point counts (Ralph et al. 1993) conducted from roads and trails at approximately 0.8 km intervals along each route. Each point count was subdivided into half-circle counts by recording birds detected on the left or right side of the road or trail because habitat types and grazing intensity often differed on each side. Although roadside sampling may confound species-habitat associations because of the influence of roadside vegetation, the three species in this study are not attracted to roadside habitat (Sutter et al., in press). Thus the occurrence of these species in the four habitat types is likely not confounded by roadside vegetation. Surveyors attended a training session prior to the study to standardize protocol and reduce surveyor bias. Surveys were conducted between 4 June and 2 July, 1994, commenced 30 minutes before sunrise, on days with no precipitation, and winds less than 20 km/hr. Each route had 20–25 stops.

Habitat associations.—Bird surveyors quantified eight measures of vegetation structure at every second native pasture point count location on the same day as the survey. Vegetation was assessed on only native pastures because of logistic constraints in sampling all habitats over a large area and because of our increased sampling of native pasture. Each surveyor laid a meter stick on the ground at least 35 m from the road/trail at a random location within each portion of the half-circle. A 6 mm diameter metal rod was passed vertically through the vegetation at each end of the meter stick and the number of contacts by different vegeta-

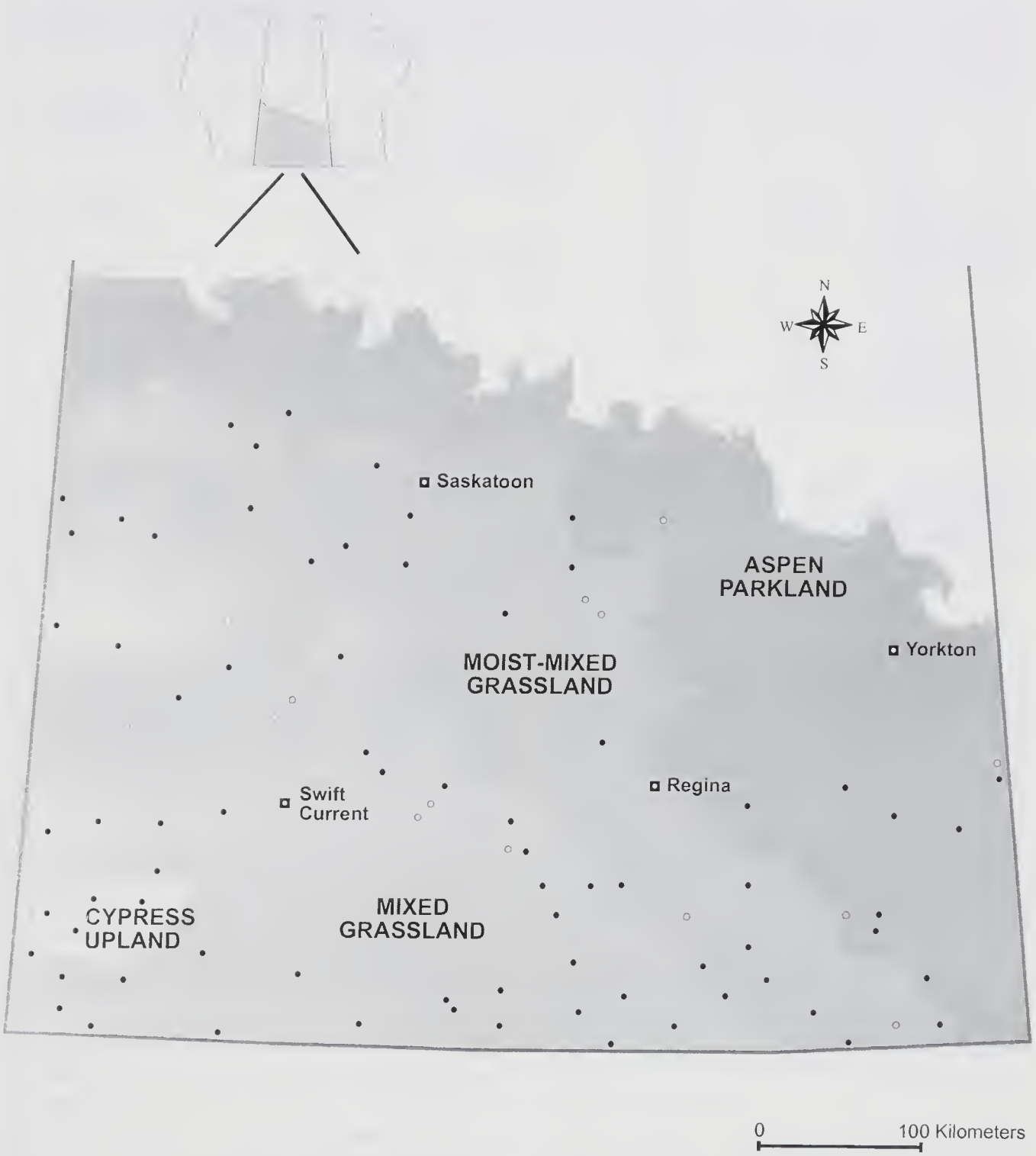

FIG. 1. Location of random (closed circles) and non-random (open circles) survey routes and ecoregions within the Prairie Ecozone of southern Saskatchewan.

tive life forms (e.g., standing dead vegetation, narrow-leaf grass, broad-leaf grass, forb, shrubs >15 cm, and dwarf shrubs <15 cm high) counted in each successive 1 decimeter (dm) height interval (Rotenberry and Wiens 1980). The occurrence of each life form was lumped into two height categories; 1 dm (number of contacts ≤1 dm) and 2+ dm (number of contacts >1 dm) height intervals because vegetation contacts in native pastures rarely occurred in the higher levels. Litter depth was measured from the surface of the ground to the top of the litter, and distance to the nearest shrub was visually estimated.

Grazing intensity was estimated in June and early July by a range ecologist as idle, lightly, moderately, or heavily grazed. Idle prairie was defined as native vegetation that had not been grazed for at least two years. Heavily grazed pastures were characterized by virtually all plant material and litter removed, greater than 20% bare soil, greater than 40% club moss, and small plants with poor vigor. Lightly grazed pasture

TABLE 1. Influence of habitat type, ecoregion, and grazing intensity on the occurrence (% half circles) of singing males in southern Saskatchewan. For each species, values followed by the same letter do not differ ($P > 0.05$) from one another.

	Sprague's Pipit	Baird's Sparrow	Chestnut-collared Longspur
	Habitat		
Native pasture (n = 1158)	18.5 A	30.5 A	21.4 A
Seeded pasture (n = 192)	14.1 A	31.2 A	17.7 A
Hayland (n = 116)	2.6 B	25.0 A	1.7 B
Cropland (n = 209)	0.5 B	5.3 B	0.5 B
	Ecoregion		
Aspen parkland (n = 238)	8.4 A	15.9 A	6.7 A
Cypress upland (n = 149)	24.2 B	16.8 A	2.0 B
Mixed grassland (n = 805)	16.9 B	25.8 B	24.4 C
Moist-mixed grassland (n = 483)	6.2 A	37.7 C	14.5 D
	Grazing intensity		
Lightly grazed (n = 112)	19.6 A	34.8	23.2
Moderately grazed (n = 137)	22.6 A	37.9	24.1
Heavily grazed (n = 81)	9.9 B	25.9	22.2

was defined as having little evidence of grazing, abundant litter and plant material, less than 10% bare soil, less than 10% club moss, and robust and vigorous plants. Moderately grazed pastures exhibited characteristics intermediate between the previous two types.

Statistical analyses.—We used songbird occurrence (presence/absence) within half-circle point counts for all analyses because more than one individual was recorded in only 9%, 8%, and 2% of the half-circle counts for Baird's Sparrow, Chestnut-collared Longspur and Sprague's Pipit, respectively. Because the two half-circle counts at any given stop do not represent independent observations, we randomly chose only one half-circle count on either side of the road or trail for inclusion in all subsequent analyses. χ^2 contingency analyses were used to determine whether the frequency of occurrence of songbirds inside half-circle point counts was influenced by land-use, grazing intensity, and ecoregion. Pair-wise comparisons were performed only for those species where the overall significance level was $P < 0.05$. Although most of the native and seeded pastures were grazed by cattle, 5% of the sample points had been idle for at least two years and were thus omitted from all analyses. A multivariate assessment of songbird occurrence in native pasture was conducted using step-wise logistic regression on half-circle point counts using vegetative structure, grazing intensity, and ecoregions. None of these variables were highly correlated with each other (all comparisons $r^2 < 0.42$, $P > 0.001$) except for the number of contacts of broad-leaf grass in the first, and 2+ decimeter categories ($r^2 = 0.71$, $P < 0.001$); thus only broad-leaf grass contacts in the first decimeter were used. Level of significance for variable inclusion in the models was set at 0.05. All analyses were performed using SAS statistical software v. 6.12 (SAS Institute Inc. 1989).

RESULTS

Land use.—The occurrence of each of the three endemic species differed significantly among habitat types (χ^2 = 59.2–75.6, df = 3, $P < 0.001$). Sprague's Pipit and Chestnut-collared Longspur occurred more frequently in native and seeded pasture than in hayland or cropland, whereas Baird's Sparrows occurred as frequently in native and seeded pastures as in hayland, but occurred least frequently in cropland (Table 1).

Distribution.—The occurrence of each species differed among ecoregions (Table 1; χ^2 = 51.1–74.4, df = 3, $P < 0.001$). Furthermore, ecoregion type was a significant predictor of occurrence in each of the three logistic regression models (Table 2). Sprague's Pipits were recorded in relatively low abundance throughout the study area, occurring most frequently in the cypress upland and mixed grassland ecoregions (Table 1). Chestnut-collared Longspurs were primarily restricted to the extreme southern portion of the province, particularly within the mixed grassland ecoregion (Tables 1, 2). Baird's Sparrows were abundant throughout much of the study area, but were recorded most frequently in the moist-mixed grassland (Tables 1, 2).

Habitat associations.—Grazing intensity had little influence on the occurrence of

TABLE 2. Results summary of step-wise logistic regression analyses of grassland songbird occurrence in native pasture. Variables are presented in the order they were entered into the model.

Species	Variable	Parameter estimate	Wald χ^2	*P*	R^2
Sprague's Pipit	Intercept	−0.894	19.922	<0.001	
	Moist-mixed grassland	−1.920	12.377	<0.001	0.092
	Heavily grazed	−0.981	4.261	0.039	
Baird's Sparrow	Intercept	−1.346	26.653	<0.001	
	Narrow-leaf grass 2+ dm	0.315	9.480	0.002	0.075
	Moist-mixed grassland	0.825	8.209	0.004	
	Shrub distance	0.008	3.941	0.002	
Chestnut-collared Longspur	Intercept	−0.605	3.664	0.055	
	Litter depth	−0.035	4.525	0.033	0.088
	Narrow-leaf grass 1 dm	−0.278	6.053	0.014	
	Mixed grassland	0.675	4.535	0.033	

Baird's Sparrow and Chestnut-collared Longspur in native pasture (Table 1; $\chi^2 = 3.4$, df = 2, $P > 0.05$ and $\chi^2 = 0.1$, df = 2, $P > 0.05$, respectively). The occurrence of Sprague's Pipits in native pasture differed significantly among grazing intensity levels ($\chi^2 = 6.2$, df = 2, $P = 0.045$). Sprague's Pipits were negatively associated with heavy grazing (Table 2), occurring twice as often in lightly and moderately grazed pastures as in heavily grazed pastures (Table 1). Although grazing intensity did not significantly influence the occurrence of Baird's Sparrows, the species was associated with pastures having greater coverage of grasses over 10 cm and were attracted to pastures with sparse shrub cover (Table 2). In contrast, Chestnut-collared Longspurs appeared to be associated with pastures that were characterized by less dense vegetative cover. The species was negatively associated with depth of the litter and the density of narrow-leaf grasses in the first decimeter (Table 2). However, the amount of variation explained by each model was extremely poor (Table 2).

DISCUSSION

Land-use.—Sprague's Pipits and Chestnut-collared Longspurs were mostly restricted to grassland habitat in southern Saskatchewan. Although we detected no differences in the frequency of occurrence of these species in native and seeded pastures, others have reported Sprague's Pipits (Owens and Myres 1973, Hartley 1994, Madden 1996, Dale et al. 1997) and Chestnut-collared Longspurs (Stewart and Kantrud 1972, Owens and Myres 1973) to prefer native prairie over a number of other habitat types. The attractiveness of seeded pastures in this study may have been influenced by the age and structural composition of the seeded pastures such that a number of these pastures may have been similar to native pastures. Indeed, surveyors consulted with the range ecologist on several occasions to confirm whether pastures were native or had been cultivated in the past. More recently seeded pastures, or those dominated by certain exotic plant species may be less suitable for Sprague's Pipits and Chestnut-collared Longspurs. In Saskatchewan, both species occur more frequently and in higher abundance in native pastures than in pastures dominated by crested wheatgrass (Sutter 1996, Davis et al. 1996, Davis and Duncan in press). Similarly, fields comprised predominantly of smooth brome grass (*Bromus inermis*) are unsuitable for these species (Wilson and Belcher 1989).

In our study, Baird's Sparrows exhibited more flexibility in their habitat use than either Chestnut-collared Longspurs or Sprague's Pipits. The occurrence of Baird's Sparrows in habitats other than native prairie has been well documented (reviewed in Davis et al. 1996) despite earlier studies that suggested the sparrow was a native prairie specialist (Cartwright et al. 1937, Owens and Myres 1973). Although we frequently recorded Baird's Sparrows in hayfields, this habitat may act as a population sink (Pulliam 1988). Using a productivity index, Dale and coworkers (1997) found significantly fewer signs of productive

behavior following mowing of hayfields in southern Saskatchewan. Mowing destroys approximately 50% of ground nests and the productivity of breeding birds in hayfields is often below that required to maintain a stable population (Frawley 1989, Bollinger et al. 1990).

Distribution and habitat associations.—We found that the distribution of Sprague's Pipit, Baird's Sparrow, and Chestnut-collared Longspur closely resembled that outlined by the Saskatchewan breeding bird atlas (Smith 1996) and the Breeding Bird Survey (BBS; Sauer et al. 1997). Additionally, our results suggest that these species are associated with certain regions within the Prairie Ecozone. Sprague's Pipits and Chestnut-collared Longspurs occurred mostly in the drier prairies of the southern portion of the province, but Chestnut-collared Longspurs were virtually absent from the cypress upland ecoregion despite the presence of large tracts of native grassland. Grassland habitat in this region is taller and denser than the surrounding grasslands (W. Harris, pers. comm.) and thus may not provide Chestnut-collared Longspurs with the short, sparse vegetative cover they require (Harris 1944, Owens and Myres 1973, Dale 1983). In contrast to Sprague's Pipits and Chestnut-collared Longspurs, Baird's Sparrows occurred most frequently in the more mesic grasslands of the moist-mixed grassland ecoregion, consistent with their overall preference for taller and denser vegetation (Dale 1983, Winter 1994, Madden 1996, Sutter and Brigham 1998, Davis and Duncan in press). Furthermore, our study indicates that the Missouri Coteau, which borders the mixed and moist-mixed grassland ecoregions, is an important landform for Baird's Sparrows in Saskatchewan (McMaster and Davis, upubl. data). This landform has also been identified as a significant region for Baird's Sparrows in North Dakota (Stewart 1975).

Grazing by livestock can have a profound influence on the structure of rangeland vegetation (Wiens and Dyer 1975, Ryder 1980). Because habitat selection by grassland birds is likely influenced by habitat structure (Wiens 1969), grazing intensity should affect the occurrence of the three songbird species examined in this study. Sprague's Pipits, and to a lesser degree, Baird's Sparrows, were both influenced by grazing intensity. Light to moderately grazed pasture has been described as preferred habitat for both Sprague's Pipits and Baird's Sparrows (Kantrud 1981; Kantrud and Kologiski 1982, 1983; Knopf 1996) although others have suggested that these species prefer idle prairie (Maher 1973, Owens and Myres 1973, Dale 1984). The latter studies, however, examined only a small number of grazed and ungrazed sites and did not discriminate between lightly or heavily grazed pastures. We could not assess the suitability of ungrazed prairie to either species in our study because this habitat type is uncommon in Saskatchewan. Despite the lack of information on the response of Sprague's Pipits and Baird's Sparrows to low intensity grazing relative to ungrazed native prairie, our results suggest that low levels of grazing intensity are tolerated by these species.

We found no difference in the response of Chestnut-collared Longspurs to grazing intensity in native pasture. Numerous studies have reported that Chestnut-collared Longspurs respond positively to grazing (Maher 1973, Dale 1983, Kantrud and Kologiski 1983, Renken and Dinsmore 1987, Bock et al. 1993). Grazing may not have influenced Chestnut-collared Longspurs in our study because the structure of the vegetation under all grazing intensities may have fallen within an acceptable range. Descriptions of Chestnut-collared Longspur breeding habitats have ranged from overgrazed pastures with sparse vegetation to situations where the ". . .thicker and taller grasses afford adequate concealment" (DuBois 1935:70). Chestnut-collared Longspurs in our study were generally associated with sparsely vegetated native pastures with low plant litter depths (see also Harris 1944, Owens and Myres 1973, Dale 1983, Johnson and Schwartz 1993).

Conservation.—While continental populations of Baird's Sparrows and Chestnut-collared Longspurs appear to be relatively stable (Sauer et al. 1997), Sprague's Pipits are currently undergoing significant population declines of 4.7% per year, one of the steepest declines recorded for grassland songbirds in North America. The conversion of native grassland to annually cropped land, and the pattern of habitat loss (i.e., habitat fragmentation) have likely played significant roles in

these declines (Davis, unpubl. data). For example, Sprague's Pipits reach their highest densities in southeastern Alberta and southwestern Saskatchewan (Sauer et al. 1997), areas characterized by large tracts of contiguous native grassland (South Digital Land Cover Project, unpubl. data). While land-use programs that convert annually tilled cropland to perennial cover will likely provide additional habitat for endemic grassland birds (Johnson and Schwartz 1993, Reynolds et al. 1994, Sutter and Brigham 1998, Davis and Duncan in press), it is imperative that the reproductive consequences of selecting alternative nesting habitats be determined to accurately assess habitat quality (Johnson and Temple 1986, Van Horne 1983, Vickery et al. 1992).

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BIRD COMMUNITIES IN NATURAL FOREST PATCHES IN SOUTHERN BRAZIL

LUIZ DOS ANJOS[1,3] AND ROBERTO BOÇON[2]

ABSTRACT.—Avifaunal composition was evaluated for natural (not artificial) patches of mixed temperate rain forest in the Campos Gerais region, Paraná State, southern Brazil. A large patch (840 ha) and 11 smaller patches (0.5–40 ha) were censused from September to December of 1995 (five hours per month, each site). The total species number was strongly correlated with patch size ($r = 0.92$, $P < 0.001$). However, the number of edge species increased with decreasing patch area; the opposite happened with forest species. Thus, the ratio of edge to forest species increased with decreasing patch area. The number of leaf insectivore species decreased the most with a decrease in area. The mean Simpson similarity index was 73.8% among forest patches of similar size. Smaller forest patches linked to the 840 ha patch were more similar to this larger patch than isolated patches. Point counts from January to December 1991 in four patches (72 points each area) showed that several species, specially trunk (and twig) insectivores and omnivores, increased in relative abundance with decreases in area of the patch (density compensation). The "habitat appropriation" hypothesis, the expansion of niches to include slightly different habitats, could explain the increased relative abundance of two trunk (and twig) insectivores: *Cranioleuca obsoleta* and *Cranioleuca pallida*. *Received 15 Oct. 1998, accepted 19 Feb. 1999.*

Forest fragmentation in the Neotropical region has been considered an important force in the loss of biodiversity (Bierregaard and Lovejoy 1989). Decreases in the number of bird species and changing avifaunal composition have been documented by many workers (Willis 1974, 1979; Karr 1982; Bierregaard 1990; Anjos 1992; Aleixo and Vielliard 1995).

Density compensation (increased relative abundance of species in biologically isolated habitats) is another frequent feature in habitat fragments (MacArthur et al. 1972, Wright 1980). Reduced competition, habitat differences, and differences in colonization (Ricklefs and Cox 1978, Blondel 1991) also have been suggested as possible reasons for density compensation in habitat fragments. Blondel and coworkers (1988) presented the "habitat appropriation" hypothesis in which populations increase on islands because of expansion into additional habitats.

Studies of birds in Neotropical forest fragments have been carried out after fragmentation took place through logging. The state of Paraná, southern Brazil, has a grassland region called "Campos Gerais" with isolated forest patches of 0.1–100 ha (Fig. 1). This landscape is natural; it was not deforested by humans. The forest patches appear in areas of suitable soil conditions surrounded by grassland and are slowly increasing in area through a natural ecological succession (Klein 1960, 1972). The forest structure among different patch series is similar (Klein 1960, Maack 1981, Klein and Hatschbach 1971). Because fragmentation has been natural, the biological processes may not have been affected by human activity. Our goal in this study was to analyze the differences in the composition of the bird community among various-sized forest patches in Campos Gerais region.

STUDY AREA AND METHODS

Study sites.—The study areas are the Fazenda Santa Rita (25° 15′ S, 49° 48′ W) and Vila Velha State Park (25° 15′ S, 49° 55′ W), Paraná State, southern Brazil, in a region called Campos Gerais (Fig. 2). The patches of forest are mixed temperate rainforest. The dominant trees are: *Araucaria angustifolia* (Araucariaceae), *Podocarpus lambertii* (Podocarpaceae), *Sebastiana commersoniana* (Euphorbiaceae), *Ocotea porosa*, and *Nectandra grandiflora* (both Lauraceae; Klein and Hatschbach 1971). The average annual temperature is 17.3° C, varying from 20.9° C during summer (December–February) and 14.1° C during winter (June–August). The range of average annual precipitation is 1500–2000 mm. Elevations range from 950–1100 m a.s.l. (Maack 1981).

Eleven forest patches (called B, C, D, E, F, G, H, I, J, L and M) from 0.5–40 ha in size and one large forest patch of 840 ha (called A) were censused. All these

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FIG. 1. Landscape in the "Campos Gerais" region, southern Brazil; grassland with naturally isolated forest patches.

sites are covered by similar forest structure. Some patches are linked (patches B, C, D, and E) to the largest forest patch (A) by forest corridors while others are completely isolated by grassland (Table 1).

Species composition.—Bird species in each patch, micro-habitat, and feeding habit were recorded during five-hour monthly visits in the morning (20 h total) September–December, 1995. Each species was classified as to its typical habitat and feeding habit through field observations and references (Fitzpatrick 1980; Belton 1984, 1985; Sick 1997; Ridgely and Tudor 1989, 1994). The habitats were categorized as open area, forest border (up to 5 m from the edge), and forest interior. We divided the forest into three levels: (1) understory (below 2 m), (2) mid-levels (2–7 m) and (3) canopy (above 7 m). Feeding habits were categorized as: omnivore, insectivore, frugivore, carnivore or nectarivore. For insectivores, the area where the insect or its larvae was most often captured was also recorded. Three classes of capture sites were defined: (1) trunk (and twigs), (2) leaves, and (3) generalized insectivores.

Relative abundance.—Relative abundance was determined by monthly point counts of unlimited distance (Blondel et al. 1970) January–December in 1991. Fifty-three points were used to calculate relative abundance: 24 in A, 12 in B, 10 in C, and 7 in G. Each point was 100 m from another and at least 50 m from the edge of the forest. Each month six points in each site were chosen at random to be sampled giving a total of 72 counts per site during the year (288 point counts total in the four sites). The relative abundance of each species was determined by dividing the total number of species contacts by the total number of points (72) sampled in each patch (Blondel et al. 1970). Sampling began at dawn at the first randomly selected point and finished about 3.5 h later at the sixth point. The time for sampling at each point was 20 min. Species were identified primarily by sound (99%). The same observer (LdA) performed all counts. Each pair or flock of each species was counted once (one contact) while vocalizing. Precautions were taken not to count the same individual or group more than once (a form was used in order to locate the counted individuals), especially highly mobile species. Bird recordings (1601 recordings of 414 species, deposited in the Bioacoustic Laboratory of the Universidade Estadual de Londrina) were used to aid identification. The observer had six years (1984–1990) of field experience in species identification in the region (Anjos 1992, Anjos and Graf 1993, Anjos et al. 1997).

Analyses.—The birds were identified mostly using the taxonomy of Meyer de Schauensee (1982) and Sick (1997). Similarities in bird species composition between forest patches were determined using the Simpson Index. β diversity (Whittaker 1960) was used to measure the degree of turnover in species composition along the six points sampled monthly (in A and G). This index is a measure of how different the samples were, in terms of the variety of species. Differ-

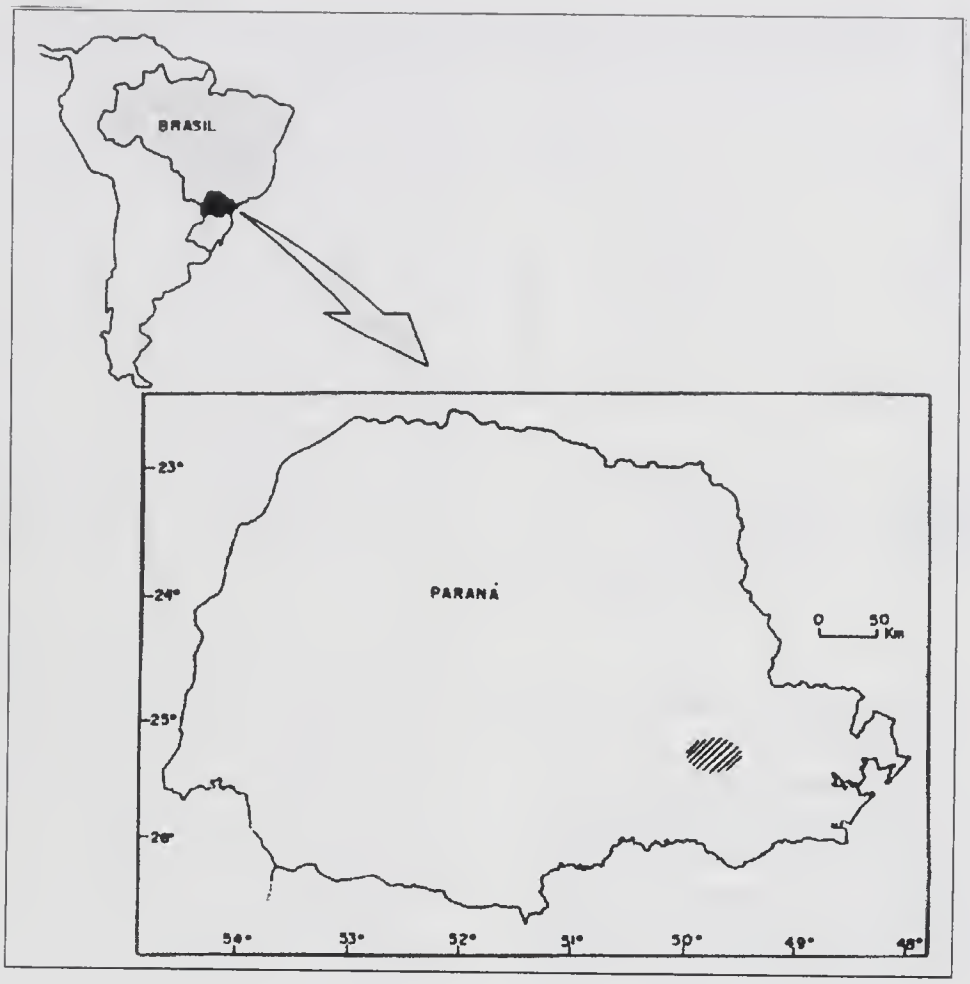

FIG. 2. Study area in "Campos Gerais" region, Paraná State, southern Brazil, indicated by hatching.

ences in numbers of species or numbers of contacts of species between the sites were tested with χ^2 analysis at $\alpha < 0.05$. Analysis of Variance (one way ANOVA) and the Tukey multiple rangc test ($P < 0.05$) were used to evaluate the average number of species and contacts recorded per sampled point in A, B, C and G. The relationship between number of bird species and size of fragment was expressed through a transformation following Preston (1962): $\log S = \log k + z\log A$ where S is the number of species and A is the size of the area. SAS/STAT (version 6.11, IBM, mainframe) was used to calculate most of the above values.

TABLE 1. Size (ha) and on the distance (m) from a continuous forest of each study site.

Site	Size	Type–Distance
A	840 ha	continuous forest
B	40 ha	linked by forest corridor–100 m
C	20 ha	linked by forest corridor–200 m
D	12 ha	linked by forest corridor–600 m
E	10.5 ha	linked by forest corridor–400 m
F	10 ha	isolated–3000 m
G	9 ha	isolated–2000 m
H	8.5 ha	isolated–800 m
I	6.5 ha	isolated–2500 m
J	4 ha	isolated–1500 m
L	1.5 ha	isolated–500 m
M	0.5 ha	isolated–1000 m

RESULTS

Habitat distribution.—Birds in all patches totaled 189 species, including 13 open area species, 51 edge species, and 125 forest species (Appendix). The open area birds used the forest only for roosting and/or for nesting but not for foraging.

There were 13 edge species in the largest patch (A) and 32 species in the 6.5 ha fragment (I). By contrast, there were 93 forest species in the largest patch and only 13 species in the smallest fragment (M; Table 2). These results indicate a general decrease in the ratio of forest to edge species with a decrease in area (Fig. 3). The exceptions are the patches E (34/21 species), G (41/28 species), and L (32/19 species). The number of understory forest species decreased faster ($\chi^2 = 15.37$, df $= 2$, $P < 0.05$) with decrease in area of forest (33 species in A, 20 species in B, and 8 spe-

TABLE 2. Number of bird speeies in the study sites aeeording their habitats and feeding habits.

	Sites											
	A	B	C	D	E	F	G	H	I	J	L	M
Habitats												
Open area	2	2	3	3	6	2	4	4	3	3	1	1
Edge	13	22	26	29	21	27	28	29	32	30	19	30
Forest/understory	33	20	8	10	5	8	8	4	10	4	7	3
Forest/mid-levels	32	29	27	22	20	17	23	18	16	15	17	6
Forest/eanopy	28	19	16	12	9	5	10	7	7	7	8	4
Feeding Habits												
Omnivores	29	32	28	31	22	19	27	28	23	24	21	16
Inseetivores/trunk	18	14	12	10	10	7	10	6	3	4	6	3
Inseetivores/leaves	30	16	16	13	9	11	15	10	11	10	8	7
Inseetivores/general	11	12	8	10	9	12	12	7	16	10	8	11
Frugivores	15	12	12	7	8	6	5	6	8	8	8	5
Carnivores	3	3	2	4	3	3	3	4	4	2	1	1
Neetarivores	2	3	2	1	0	1	1	1	3	1	0	2
Total Speeies	108	92	80	76	61	59	73	62	68	59	52	45

cies in C) than mid-level forest species (32 species in A, 29 species in B, and 27 species in C; $\chi^2 = 0.43$, df = 2, $P > 0.05$); canopy forest species were intermediate in the ratio of decreasing (28 species in A, 19 species in B, and 16 species in C; $\chi^2 = 3.71$, df = 2, $P > 0.05$; Table 2).

Similarity between sites.—The similarity index (Simpson) between the largest site (A: 108 species) and the smallest (M: 45 species) was 40% (17 species common to both sites); however, the mean was 73.8 ± 2.7% (SE) among forest patches of similar size.

The number of species was correlated with area (Fig. 4; $r = 0.92$, df = 10, $P < 0.001$). Species living in open areas were not considered in this analysis; edge species were included with forest species because the majority of them were commonly found within the forest. The number of species can be predicted according to the Preston (1962) model: log$S$ = 3.81 + 0.17 log$A$, where S is the number of species and A is the fragmented area in ha.

Feeding habits.—Of the 189 species recorded, 85 were insectivores, 58 omnivores, 28 frugivores, 12 carnivores, and 6 nectarivores. Among the insectivores, 33 were leaf insectivores, 31 generalized insectivores (capture insects in various ways), and 21 trunk insectivores.

Insectivores were less abundant in B (40 ha;

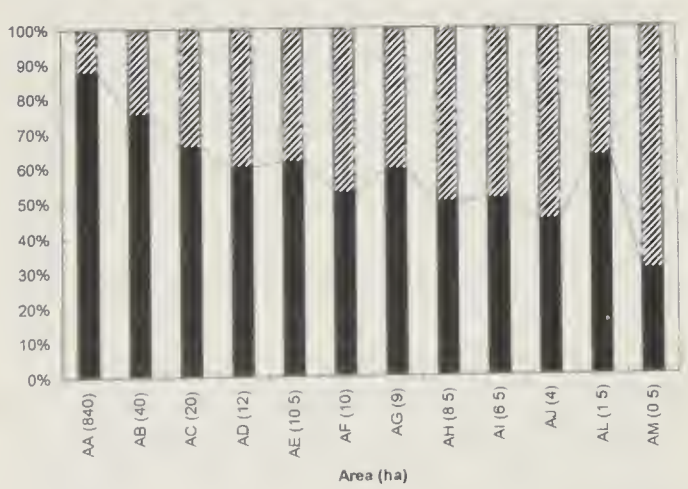

FIG. 3. Ratio of forest (solid) and edge (hatehed) speeies in the study sites. Sites B–E linked to A by forest corridors.

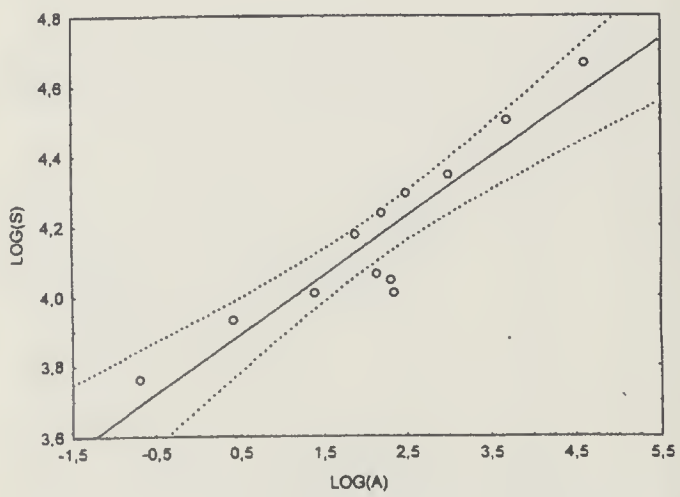

FIG. 4. Correlation (log/log) between number of speeies (S) and area (A) of fragment. Dotted lines indieate 95% eonfidenee interval.

42 species) than in A (840 ha; 59 species) although not significantly so ($\chi^2 = 2.86$, df = 1, $P > 0.05$). In patches smaller than 40 ha the rate of decrease slowed as patch size diminished (36 species/20 ha, 33 species/12 ha, 28 species/10.5 ha); in patches smaller than 10.5 ha, there was no clear pattern (Table 2). The greatest reduction in species occurred in leaf insectivores, from 30 species in the forest (A) to 16 species in the largest patch (B; $\chi^2 = 4.26$, df = 1, $P < 0.05$); the loss of trunk insectivores was not so great (18 species in A and 14 species in B; $\chi^2 = 0.5$, df = 1, $P > 0.05$) while generalized insectivores gained one species (11 species in A and 12 species in B).

Omnivores were represented by two more species in B (32 species) than in A (30 species). Their numbers remained relatively constant down through the 12 ha patch (D; 31 species) but decreased in smaller patches (Table 2).

Frugivores decreased slightly in number ($\chi^2 = 0.46$, df = 2, $P < 0.05$) from A (15 species) to B and C (both with 12 species). The number of frugivores stayed between 5 and 8 species in patches smaller than 12 ha (Table 2).

Carnivores and nectarivores were represented by few species in all sites (1–4 species; Table 2).

Number of species and contacts.—In point counts conducted in 1991 we recorded 138 species in A, 125 in B, 103 in C, and 91 in G. The average numbers of species per sampled point were: 23.6 in A, 16.5 in B, 18.5 in C, and 21.4 in G. The number of species per sampled point was not significantly different (Tukey test: $P > 0.05$) between A and G although they are different in the size and total number of species recorded. The intermediate-sized patches B (40 ha) and C (20 ha) did not show significant differences (Tukey test: $P > 0.05$) among the numbers of species per sampled point, but both were significantly different from A and G (Tukey test: $P < 0.05$).

The average numbers of contacts per sampled point were: 27.0 in A, 19.1 in B, 22.1 in C, and 25.8 in G. The numbers of contacts per point were not significantly different between A and G nor between B and C; but they were significantly different between A–B, A–C, G–B and G–C (Tukey test: $P < 0.05$).

There were variations in the average number of contacts during the year in the four study sites. The number of contacts was highest in September/October–January than February–August (Fig. 5).

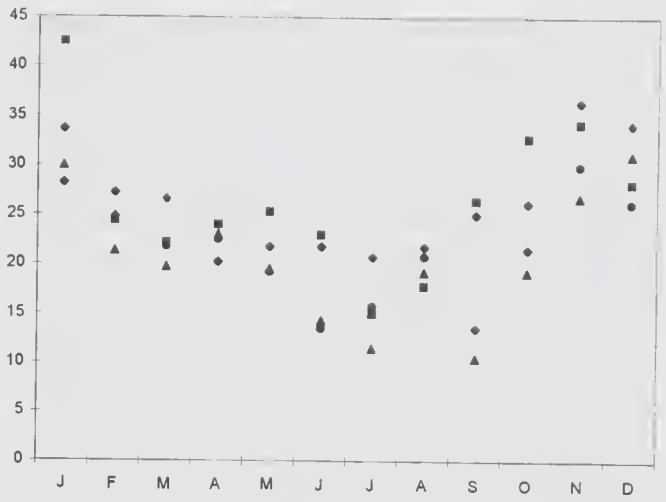

FIG. 5. Average number of contacts in the studied sites during the year. Square = A, triangle = B, circle = C, diamond = G.

Relative abundance.—The highest relative abundance (number of contacts divided by the number of sampled points) in this study was *Basileuterus leucoblepharus* (1.2) followed by *Turdus rufiventris* (0.85), *Lepidocolaptes squamatus* (0.68), *Basileuterus culicivorus* (0.68), *Cyclarhis gujanensis* (0.67), and *Cranioleuca obsoleta* (0.61).

The majority of species recorded in the point counts presented significant differences in the values of relative abundance when occurring in three or four sampled sites (indicated with "s" in Appendix; df = 2 or 3, $P < 0.05$). Some of these species increased in abundance with the decrease in area (density compensation) such as *Veniliornis spilogaster, Cranioleuca obsoleta, Turdus amaurochalinus, Cyclarhis gujanensis, Parula pitiayumi, Thraupis sayaca,* and *Stephanophorus diadematus.* The distribution of the abundances in a rank order showed that the 12 species with highest abundances (indicated with an * in Appendix) in the smallest patch analyzed (G) comprised 27% of total contacts but they comprised only 20% in the continuous forest (A).

Relative abundance increased with decreasing area for 12 omnivorous species (Appendix): *Penelope obscura* ($\chi^2 = 9.12$, df = 3, $P < 0.05$), *Pachyramphus polychopterus* ($\chi^2 = 73.87$, df = 3, $P < 0.001$), *Pitangus sulphuratus* ($\chi^2 = 106.39$, df = 3, $P < 0.001$), *Elaen-*

ia mesoleuca ($\chi^2 = 23.38$, df = 3, $P < 0.001$), *Cyanocorax caeruleus* ($\chi^2 = 21.08$, df = 3, $P < 0.001$), *Turdus rufiventris* ($\chi^2 = 8.52$, df = 3, $P < 0.05$), *Turdus amaurochalinus* ($\chi^2 = 23.9$, df = 3, $P < 0.001$), *Cyclarhis gujanensis* ($\chi^2 = 36.19$, df = 3, $P < 0.001$), *Stephanophorus diadematus* ($\chi^2 = 12.92$, df = 3, $P < 0.01$), *Thraupis sayaca* ($\chi^2 = 19.8$, df = 3, $P < 0.001$), *Zonotrichia capensis* ($\chi^2 = 33.64$, df = 3, $P < 0.001$), and *Carduelis magellanicus* ($\chi^2 = 14.07$, df = 3, $P < 0.01$). The sum of relative abundances of the omnivorous species increased ($\chi^2 = 28.41$, df = 2, $P < 0.001$) from A (6.56) to the patches C (7.52) and G (9.0).

The sum of relative abundances of leaf insectivorous species was highest ($\chi^2 = 77.15$, df = 3, $P < 0.001$) in A (8.42), followed by G (6.18), C (5.56), and B (5.14). *Parula pitiayumi* ($\chi^2 = 12.86$, df = 3, $P < 0.01$) increased in relative abundance with decreases in area (Appendix).

The sum of relative abundances of species of trunk insectivores increased ($\chi^2 = 10.8$, df = 1, $P < 0.01$) from A (4.06) to G (5.24) as the result of a substantial increase in relative abundance of two species: *Cranioleuca obsoleta* (0.21 in A and 1.54 in G) and *C. pallida* (0.14 in A and 0.93 in G).

Relative abundances of *Furnarius rufus* ($\chi^2 = 49.89$, df = 2, $P < 0.001$), *Tyrannus melancholicus* ($\chi^2 = 23$, df = 3, $P < 0.001$), and *Phyllomyias fasciatus* ($\chi^2 = 39.72$, df = 3, $P < 0.001$) generalized insectivores, increased with decreases in area (Appendix). The sum of the relative abundances of this group was higher ($\chi^2 = 8.43$, df = 1, $P < 0.01$) in G (3.82) than A (2.93).

The sum of the relative abundances of frugivores decreased quickly ($\chi^2 = 176.93$, df = 3, $P < 0.001$) with decreases in area: A, 4.18; B, 2.89; C, 1.76, and G, 0.92. Only *Leptotila verreauxi* ($\chi^2 = 20.43$, df = 3, $P < 0.001$) and *L. rufaxilla* ($\chi^2 = 11.96$, df = 3, $P < 0.01$) increased in relative abundance.

DISCUSSION

Number of species.—Based on censuses from a few visits to many islands in the species/area studies, Haila and Järvinen (1981: 561) suggested that the "gain by increasing the number of visits to an island is the improved accuracy in the recording of rare species." Almost 90% of the species in a site are recorded during a single visit (Haila and Kuusela 1982). Taking into account the point counts of one year carried out in the present study, the combined samplings in A, B, C, and G from September to December (four visits) revealed 73–78% of the total species in these sites; this is less than the 90% predicted by Haila and Kuusela (1982). The fewer species we recorded in four visits is problably due to a higher proportion of rare species in our study sites. Therefore researchers in the Neotropical region, especially in forests, should make several visits to a site instead of a single visit.

There was a strong correlation ($r = 0.92$, df = 10, $P < 0.001$) between the number of bird species and the size of the forest patches in the Campos Gerais region. Other effects, such as habitat heterogeneity, might be more important than area in predicting the number of species found on an island (Martin et al. 1995). In more homogeneous sites it is expected that the effect of area would increase (Connor and McCoy 1979). Galli and coworkers (1976) studied woodlots in New Jersey with similar foliage height diversity and found a strong correlation between the number of species and size of the area. Martin (1981) studied homogeneous shelterbelts in South Dakota and concluded that area was the most important factor in determining the number of species. The similarity in vegetation structure between Campos Gerais forest patches is due to their being at approximately the same stage of ecological succession (Klein 1960, 1972; Klein and Hatschbach 1971; Maack 1981), and probably explains the high species/area correlation.

Based on the study by Tomialojc and coworkers (1984) in Poland, Blondel (1986) suggested that the habitats in large forests appear to be broken into a mosaic of "sink" and "source" because a large forest is represented by a mosaic of habitat patches. This results in a potential heterogeneity of the distribution of birds in large forests. In order to test the source/sink (Blondel 1986) role of larger forests, we calculated the β-diversity (Whittaker 1960) among the six points sampled monthly, in the 9 ha patch (G) and in the largest patch (A, 840 ha). The mean β-diversity was higher in A (1.68) than in G (1.27; Mann-Whitney

U-test: $U = 12.5$, $P < 0.05$), which suggests a more homogeneous bird distribution in the smaller area. The average number of species per point sampled was not significantly different (Tukey test: $P > 0.05$) between G and A, which suggests that the higher number of total species in the largest patch is mainly due to the heterogeneity of species' distributions compared to smaller patch.

It was expected that there would be more species in A (138 species, 840 ha) than in G (91 species, 9 ha) because of the difference in size of the fragments. The small difference can be explained by the heterogeneity of species distribution in A; the area sampled in A (24 sampled points, which represents around 80 ha) corresponds to about 10% of the total site, but the total area of G (9 ha) was sampled. Two hundred and seven species were recorded in A in a parallel study (Anjos 1992). Thus, the heterogeneity in bird distribution resulted in just 67% of the total avifauna in A being recorded in this study.

Composition of the bird communities.—In the Neotropics, as in the rest of the world, losses of species and changes in avian community composition occur with fragmentation of forest areas. In the Campos Gerais, the scarcity of forest species are, in part, balanced by gains in edge species (Fig. 3). Willis (1979) pointed out that the woodlots of São Paulo, southeastern Brazil, have become more like temperate zone forests with an emphasis on oscine birds characteristic of canopy and edge. Bierregaard and Lovejoy (1988) noted some edge species (*Troglodytes aedon* and *Ramphocelus carbo*) wandering into small forest patches (1 ha) after experimental deforestation in Amazonia. In the Campos Gerais region a gradual increase in the ratio of edge species to forest species was obvious with a decrease in fragment area. The majority of these edge species are oscines, some of them living in the canopy.

The proportion of forest/edge species does not seem to be related only to the size of the area. MacArthur and Wilson (1963, 1967) demonstrated that isolation is also an important factor. Among the isolated patches, L (1.5 ha) possessed a higher proportion of forest species than F (10 ha), H (8.5 ha), I (6.5 ha), or J (4 ha) probably because it was closer to the largest patch (Fig. 3, Table 1).

Among forest birds, the principal decrease in number of species in the Campos Gerais patches was associated with the loss of understory species. Canopy species probably fly to a nearby patch when there is a shortage of resources. Bierregaard and Lovejoy (1989) verified a decrease in the number of species also occurring among understory birds in Amazonia.

Aleixo and Vielliard (1995) pointed out that leaf insectivores of the understory were those most likely to be absent in a woodlot of 251 ha in São Paulo. We also found that most of the understory species that were absent from the small patches in the Campos Gerais region were leaf insectivores. Trunk insectivores were rarely found in small woodlots by Willis (1979); these were mostly small birds, such as *Picumnus* spp. (12 g) and *Veniliornis spilogaster* (43 g). Large trunk insectivores, such as *Phloeoceastes robustus* (263 g) and *Dryocopus lineatus* (246 g), were recorded only in the forest of our study. Only small or mid-size species such as *Cranioleuca obsoleta* (14 g), *C. pallida* (12 g), *Lepidocolaptes squamatus* (28 g), and *Veniliornis spilogaster* were recorded in the smallest patches (Appendix).

Frugivores were rare in small patches of forest of Amazonia (Bierregaard and Lovejoy 1989) and São Paulo (Willis 1979, Aleixo and Vielliard 1995). Willis (1979) thought that because frugivores can easily travel to other woodlots to look for available resources they probably disappear from the small woodlots; they depend on scattered trees of different species at different seasons or years, and only large woodlots have enough tree diversity to support them. Frugivores occurred in all the patches we studied in the Campos Gerais region. This ability to easily move between patches may have prevented their numbers from declining (although the relative abundance of frugivores in smaller patches was low, as shown above).

Omnivores, which can switch from fruit to insects or vice versa, may benefit from small woodlots of São Paulo (Willis 1979). This group was represented by the greatest number of species in the Campos Gerais and tended to increase its contribution to the avifaunal composition with decreases in area; the sum of relative abundance increased from A (6.56) to G (9.0).

The present composition of the avifauna in the patches at the Campos Gerais region is the result of a long period during which, presumably, many factors have operated. Forest patches resulting from human disturbance of a continuous forest are isolated more rapidly. The effects of isolation on natural and artificial forest fragments may be different. According to Willis (1979), frugivores seem to be more sensitive to isolation in woodlots in São Paulo than in those of the Campos Gerais. But the woodlots studied by Willis (1979) are larger and more isolated than the patches studied in Campos Gerais. Thus, a study carried out under similar conditions is necessary for a more precise comparative analysis.

Relative abundance.—Vielliard and Silva (1990) and Aleixo and Vielliard (1995), using the same census method of point counts in São Paulo, Brazil, obtained a similar pattern of monthly variation in number of contacts as we did (Fig. 5). This is probably because September–December is the main period when all the species are more obvious when they breed and vocalize (Vielliard and Silva 1990, Aleixo and Vielliard 1995). There are also summer transients of some species in the study area from September to March (Anjos and Graf 1993). Therefore, counts of relative abundance are influenced by vocalization and migratory behavior. Because censuses were performed monthly in each patch, seasonal variation was assumed to be the same for all sites, making comparative analysis possible between the patches. In addition, because habitat physiognomy was similar for all of our patches, bias between the sites resulting from differences in detection of vocalizations (Schieck 1997) was unlikely.

Density compensation was detected in the present study for several species. For edge species the greater relative abundance is probably due to the relatively greater habitat area in the smaller patches. Edge species may also be better colonizers of isolated patches than forest species.

Decreased competition in smaller patches could explain density compensation (Ricklefs and Cox 1978). This seems to be the case for two leaf insectivores (*Thamnophilus caerulescens* and *Parula pitiayumi*) and some trunk insectivores (*Veniliornis spilogaster, Lepidocolaptes squamatus, Cranioleuca obsoleta,* and *C. pallida*) in the present study. These groups decreased in number of species as area decreased, which could mean fewer competitors. However, documenting that competition occurs among species is not easy (Wiens 1989).

The "habitat appropriation" hypothesis of Blondel and coworkers (1988; a population size increases in an island because of an expansion of habitat occupation) was examined with two trunk and twig insectivores. *Cranioleuca obsoleta* ($\chi^2 = 162.72$, df = 3, $P < 0.05$) and *C. pallida* ($\chi^2 = 91.41$, df = 3, $P < 0.05$) increased in relative abundance with decreases in area (Appendix). Points were selected in A and G with either dense or open understory. The relative abundance of the two species was calculated in these two habitats (dense and open understory). *Cranioleuca obsoleta* had a relative abundance of 0.33 in open understory and 0.08 in dense understory areas of the 840 ha patch (A) but 2.07 and 1.06, respectively, in the 9 ha patch (G). *Cranioleuca pallida* was not observed in dense understory and had a relative abundance of 0.67 in open understory areas of A, and 0.43 and 1.29 respectively in G. This suggests that both species increase the habitats they use (they tended to be more abundant in areas of dense understory in G). These results were consistent with what could be interpreted as the "habitat appropriation" hypothesis. This should be considered as a complementary explanation for density compensation. *Cranioleuca obsoleta* also was common with high relative abundance in another natural patch of forest in Curitiba city, Paraná (Anjos and Laroca 1989).

The causes of density compensation are not clear but they may be different for each species.

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APPENDIX. Relative abundance of the bird species in the sites A, B, C, and G; (s) indicates significant difference (χ^2, $P < 0.05$) between the number of contacts when it is recorded in at least 3 sites and (*) indicates the first 12 species with highest values of relative abundance in each site. Only the occurrence (1) is indicated for other sites.

Family Species	Sites												[a]Habitat	[b]Habit
	A	B	C	G	D	E	F	H	I	J	L	M		
TINAMIDAE														
Crypturellus obsoletus (s)	0.472	0.113	0.028										FU	OM
ARDEIDAE														
Syrigma sibilatrix		0.097	0.153	0.194	1	1		1		1			OA	OM
THRESKIORNITHIDAE														
Theristicus caudatus	0.361	0.306	0.403	0.278		1		1			1		OA	OM
CATHARTIDAE														
Coragyps atratus	0.014		0.042	0.042	1	1	1	1	1	1	1		OA	CA
Cathartes aura					1	1	1	1					OA	CA
ACCIPITRIDAE														
Buteo albicaudatus				0.028									OA	CA
Buteo magnirostris (s)	0.042	0.081	0.056	0.222	1	1	1	1	1	1		1	ED	CA
Heterospizias meridionalis				0.083									OA	CA
FALCONIDAE														
Herpetotheres cachinnans		0.016											FC	CA
Micrastur ruficollis	0.111												FC	CA
Milvago chimachima		0.016	0.097	0.056	1	1		1		1	1		ED	OM
Polyborus plancus (s)	0.083	0.032	0.153	0.138	1	1	1	1	1	1	1		ED	OM
Falco femoralis										1			OA	CA
Falco sparverius						1							OA	GI
CRACIDAE														
Penelope obscura (s)	0.014	0.032	0.069	0.125	1	1	1	1	1	1	1		FM	OM
PHASIANIDAE														
Odontophorus capueira (s)	0.125	0.048	0.014										FU	OM
RALLIDAE														
Aramides saracura	0.028	0.048			1								FU	OM

APPENDIX. CONTINUED.

Family Species	Sites												[a]Habitat	[b]Habit
	A	B	C	G	D	E	F	H	I	J	L	M		
COLUMBIDAE													FC	FR
Columba speciosa		0.065											ED	FR
Columba picazuro (s)	0.111	0.113	0.417	0.167	1	1	1	1	1	1	1	1	FC	FR
Columba maculosa			0.014					1					ED	FR
Columba cayennensis	0.014	0.016	0.042	0.069									FC	FR
Columba plumbea	0.111	0.016											ED	FR
Zenaida auriculata				0.014	1	1	1	1	1	1	1	1	ED	FR
Columbina talpacoti		0.097			1		1	1	1	1		1	FU	FR
Leptotila verreauxi (s)	0.014	0.290	0.056	0.167	1		1		1	1	1	1	FU	FR
Leptotila rufaxilla (s)	0.014	0.081	0.083	0.181			1		1	1	1		FU	FR
Geotrygon montana	0.306	0.113												
PSITTACIDAE													FC	FR
Pyrrhura frontalis (s)	0.611*	0.290	0.361	0.042	1	1					1		ED	FR
Forpus xanthopterygius	0.014												FC	FR
Brotogeris tirica (s)	0.222	0.016	0.014										FC	FR
Pionopsitta pileata	0.250		0.028			1							FC	FR
Pionus maximiliani	0.181	0.145	0.054	0.139				1			1		FC	FR
Amazona aestiva		0.016	0.014	0.028					1	1			FC	FR
Amazona vinacea	0.014		0.028	0.014										
CUCULIDAE													FM	OM
Coccyzus americanus	0.069	0.016											FM	OM
Piaya cayana	0.056	0.032	0.111		1	1	1	1	1		1		ED	OM
Guira guira				0.014	1			1					ED	OM
Tapera naevia			0.028								1			
TYTONIDAE													ED	CA
Tyto alba									1					
STRIGIDAE													FC	CA
Otus choliba					1			1					ED	CA
Glaucidium brasilianum	0.056												ED	CA
Strix hylophila		0.016		0.014										
CAPRIMULGIDAE													ED	GI
Lurocalis semitorquatus	0.069	0.016		0.028										

APPENDIX. CONTINUED.

Family Species	Sites												[a]Habitat	[b]Habit
	A	B	C	G	D	E	F	H	I	J	L	M		
TROCHILIDAE														
Phaethornis pretrei	0.028	0.032	0.014										FU	NE
Colibri serrirostris		0.016							1			1	ED	NE
Stephanoxis lalandi			0.056										ED	NE
Chlorostilbon aureoventris		0.081		0.014					1	1		1	ED	NE
Thalurania glaucopis	0.042	0.032	0.014										FU	NE
Leucochloris albicollis	0.056	0.081	0.097	0.167	1		1	1	1				FM	NE
TROGONIDAE														
Trogon rufus	0.014	0.016											FM	OM
Trogon surrucura	0.250	0.226	0.097		1								FM	OM
RAMPHASTIDAE														
Ramphastos dicolorus	0.097	0.032	0.028										FC	FR
PICIDAE														
Picumnus nebulosus (s)	0.014		0.042	0.292	1	1		1					FM	TI
Picumnus temminckii	0.056	0.081	0.042	0.111	1	1	1						FM	TI
Colaptes campestris (s)		0.032	0.306	0.528	1	1	1	1	1	1	1	1	ED	TI
Colaptes melanochloros	0.056	0.016	0.014										FC	TI
Piculus aurulentus (s)	0.069	0.032	0.264	0.028	1	1	1				1		FM	TI
Dryocopus lineatus	0.014												FC	TI
Melanerpes flavifrons	0.139	0.016											FC	TI
Leuconerpes candidus							1						ED	TI
Veniliornis spilogaster (s)	0.347	0.226	0.403	0.500	1	1	1	1	1	1	1		FM	TI
Phloeoceastes robustus	0.028												FC	TI
DENDROCOLAPTIDAE														
Dendrocincla turdina	0.028												FM	TI
Sittasomus griseicapillus (s)	0.972*	0.870*	0.389	0.028	1	1							FM	TI
Xiphocolaptes albicollis	0.056	0.064											FM	TI
Dendrocolaptes platyrostris (s)	0.542*	0.291	0.319	0.292	1	1					1		FM	TI
Lepidocolaptes angustirostris	0.056	0.081	0.083	0.097									FM	TI
Lepidocolaptes squamatus (s)	0.639*	0.435*	0.819*	0.806*	1	1	1	1			1	1	FM	TI
Lepidocolaptes fuscus (s)	0.403	0.226	0.056	0.083									FM	TI

APPENDIX. CONTINUED.

Family Species	Sites												[a]Habitat	[b]Habit
	A	B	C	G	D	E	F	H	I	J	L	M		
FURNARIIDAE														
Clibanornis dendrocolaptoides	0.028			0.014	1		1		1				FU	GI
Furnarius rufus (s)		0.032	0.611*	0.819*	1	1	1	1	1	1		1	ED	GI
Leptasthenura striolata (s)	0.042	0.016	0.139	0.097									FC	LI
Leptasthenura setaria (s)	0.680*	0.048	0.847*	0.264	1	1	1		1				FC	LI
Synallaxis ruficapilla	0.139	0.081			1								FU	LI
Synallaxis spixi			0.042	0.042	1		1	1	1			1	FU	LI
Synallaxis cinerascens (s)	0.333	0.419*	0.181	0.014					1	1			FU	LI
Cranioleuca obsoleta (s)	0.208	0.081	0.528	1.542*	1	1	1	1	1	1	1	1	FM	TI
Cranioleuca pallida (s)	0.139	0.032	0.444	0.931*				1		1			FM	TI
Anumbius annumbi			0.236	0.278	1	1	1		1	1		1	ED	GI
Syndactyla rufosuperciliata (s)	0.431	0.258	0.417	0.167	1	1	1	1	1	1	1		FM	LI
Anabacerthia amaurotis	0.153	0.065	0.042	0.056									FM	LI
Philydor rufus (s)	0.375	0.145	0.125										FC	LI
Heliobletus contaminatus	0.208	0.145	0.222		1	1							FM	TI
Xenops rutilans	0.083	0.032	0.028										FM	TI
Xenops minutus	0.069	0.032											FM	LI
Sclerurus scansor	0.194	0.016									1		FU	GI
Lochmias nematura	0.167	0.048			1			1	1	1			FU	GI
FORMICARIIDAE														
Batara cinerea	0.055												FU	OM
Mackenziaena leachii	0.014	0.016											FU	OM
Biatas nigropectus	0.028												FM	LI
Thamnophilus caerulescens (s)	0.402	0.371	0.667*	0.403	1	1	1	1	1	1	1	1	FM	LI
Dysithamnus mentalis (s)	0.375	0.274	0.042	0.083									FM	LI
Drymophila malura	0.181	0.161											FU	LI
Pyriglena leucoptera	0.111	0.032											FU	LI
Chamaeza campanisoma	0.764*	0.177											FU	OM
Chamaeza ruficauda	0.653*	0.161											FU	OM
Hylopezus nattereri	0.139	0.048											FU	GI
Conopophaga lineata	0.333	0.323		0.194	1	1	1		1		1		FU	GI

APPENDIX. CONTINUED.

Family Species	Sites												[a]Habitat	[b]Habit
	A	B	C	G	D	E	F	H	I	J	L	M		
COTINGIDAE														
Pachyramphus viridis	0.014												FM	OM
Pachyramphus castaneus	0.014	0.016											FM	OM
Pachyramphus polychopterus (s)	0.056	0.129	0.556*	0.667*	1	1	1	1	1	1	1		FM	OM
Platypsaris rufus	0.111	0.016	0.069		1		1		1	1	1		FM	OM
Tityra cayana	0.181	0.129											FC	FR
Procnias nudicollis (s)	0.583*	0.210	0.278										FC	FR
PIPRIDAE														
Chiroxiphia caudata (s)	0.681*	0.565*	0.083			1					1		FM	FR
Schiffornis virescens	0.347	0.403				1							FU	FR
TYRANNIDAE														
Xolmis cinerea									1				OA	GI
Colonia colonus	0.014												FC	GI
Knipolegus lophotes												1	OA	GI
Knipolegus nigerrimus						1							OA	GI
Knipolegus cyanirostris				0.014									OA	GI
Muscipipra vetula	0.014												ED	GI
Satrapa icterophrys						1	1		1	1		1	ED	GI
Machetornis rixosus									1	1		1	ED	GI
Tyrannus savana		0.016	0.014				1	1	1	1		1	ED	GI
Tyrannus melancholicus (s)	0.042	0.016	0.222	0.236	1		1	1	1	1	1	1	ED	GI
Empidonomus varius		0.016	0.028	0.069				1	1				ED	GI
Megarhynchus pitangua	0.125									1			FC	LI
Myiodynastes maculatus (s)	0.139	0.048	0.056	0.208	1			1			1	1	FC	OM
Pitangus sulphuratus (s)	0.028	0.193	0.917*	1.042*	1	1	1	1	1	1	1	1	ED	OM
Myiarchus swainsoni (s)	0.125	0.097	0.500	0.583	1		1	1	1	1	1	1	ED	LI
Contopus cinereus			0.014										FM	GI
Empidonax euleri	0.361	0.290	0.292	0.319	1		1		1		1		FU	GI
Cnemotriccus fuscatus	0.028	0.065	0.028	0.028									FU	GI
Myiopholbus fasciatus		0.016		0.139	1	1	1		1	1	1	1	ED	GI
Hirundinea ferruginea												1	OA	GI
Platyrinchus mystaceus (s)	0.403	0.161		0.306									FU	LI

APPENDIX. CONTINUED.

Family Species	Sites												[a]Habitat	[b]Habit
	A	B	C	G	D	E	F	H	I	J	L	M		
Tolmomyias sulphurescens	0.292	0.065											FC	LI
Todirostrum plumbeiceps	0.014				1	1		1					FU	LI
Idioptilon nidipendulum	0.028												FU	LI
Myiornis auricularis	0.014	0.032											FU	LI
Hemitriccus obsoletus	0.167	0.048											FM	LI
Pogonotriccus eximius (s)	0.333	0.161	0.042	0.194									ED	LI
Phylloscartes ventralis (s)	0.431	0.290	0.694*	0.542	1	1	1	1	1	1	1	1	FM	LI
Phylloscartes oustaleti	0.097												ED	LI
Serpophaga subcristata (s)	0.014		0.056	0.236	1		1			1			ED	OM
Elaenia parvirostris			0.056	0.097	1			1	1	1		1	ED	OM
Elaenia mesoleuca (s)	0.042	0.065	0.264	0.292	1		1	1	1	1	1	1	ED	OM
Elaenia chiriquensis				0.014									ED	OM
Elaenia obscura		0.032	0.069	0.028	1			1					FC	LI
Myiopagis caniceps	0.056												FC	GI
Camptostoma obsoletum	0.153	0.113	0.222	0.250	1	1	1	1	1		1	1	FC	GI
Phyllomyias fasciatus (s)	0.014	0.016	0.292	0.333									FM	LI
Acrochordopus burmeisteri	0.042		0.069										FU	LI
Leptopogon amaurocephalus	0.111												FU	FR
Pipromorpha rufiventris	0.167	0.016				1								
CORVIDAE														
Cyanocorax caeruleus (s)	0.403	0.194	0.208	0.556	1	1							FC	OM
Cyanocorax chrysops			0.014						1	1	1		FM	OM
TROGLODYTIDAE														
Troglodytes aedon			0.083	0.167	1	1	1	1	1	1	1	1	ED	LI
TURDIDAE														
Platycichla flavipes		0.048						1	1				FM	OM
Turdus nigriceps			0.014	0.097	1			1	1	1			FM	OM
Turdus rufiventris (s)	0.611*	0.887*	0.847*	1.042*	1	1	1	1	1	1	1	1	FM	OM
Turdus amaurochalinus (s)	0.014	0.113	0.194	0.319	1	1	1	1	1	1	1	1	FM	OM
Turdus albicollis	0.486	0.354	0.264	0.486	1	1	1	1	1		1		FU	OM

APPENDIX. CONTINUED.

Family Species	Sites												[a]Habitat	[b]Habit
	A	B	C	G	D	E	F	H	I	J	L	M		
VIREONIDAE														
Cyclarhis gujanensis (s)	0.361	0.419*	0.944*	0.917*	1	1	1	1	1	1	1	1	FM	OM
Vireo olivaceus	0.416	0.500*	0.444	0.597*	1	1	1	1	1	1	1		FC	GI
Hylophilus poicilotis	0.500	0.419*	0.361		1	1							FC	OM
CICTERIDAE														
Molothrus bonariensis				0.028					1	1		1	ED	OM
Cacicus haemorrhous	0.139	0.065											FC	OM
Cacicus chrysopterus	0.222	0.242	0.389	0.319	1	1							FC	OM
Gnorimopsar chopi		0.016	0.306	0.153	1	1					1	1	ED	OM
PARULIDAE														
Parula pitiayumi (s)	0.528	0.403*	0.667*	0.778*	1	1	1	1	1	1	1	1	FC	LI
Geothlypis aequinoctialis							1		1	1	1	1	ED	GI
Basileuterus culicivorus (s)	1.056*	0.565*	0.111	0.972*	1	1	1	1	1	1	1		FM	LI
Basileuterus leucoblepharus (s)	1.264*	1.419*	0.833*	1.278*	1	1	1	1	1		1	1	FU	LI
TERSINIDAE														
Tersina viridis	0.014	0.016	0.056	0.097	1	1	1	1	1	1	1		ED	FR
THRAUPIDAE														
Euphonia musica	0.014		0.014		1				1	1	1		FC	FR
Euphonia pectoralis	0.014	0.048											FC	FR
Euphonia chalybea	0.014	0.032											FC	FR
Pipraeidea melanonota	0.056	0.081	0.167	0.153		1	1	1		1			FM	OM
Tangara preciosa	0.208	0.177	0.194										FC	FR
Stephanophorus diadematus (s)	0.153	0.242	0.264	0.444	1	1		1					ED	OM
Thraupis sayaca (s)	0.069	0.032	0.181	0.278	1		1	1	1	1	1	1	FC	OM
Thraupis bonariensis								1				1	ED	OM
Habia rubica	0.111	0.081											FU	OM
Tachyphonus coronatus	0.111	0.048											FM	OM
Trichothraupis melanops	0.028	0.081											FM	OM
Pyrrhocoma ruficeps	0.014												FU	GI
Hemithraupis ruficapilla	0.097												FC	GI

APPENDIX. CONTINUED.

Family Species	Sites												[a]Habitat	[b]Habit
	A	B	C	G	D	E	F	H	I	J	L	M		
FRINGILLIDAE														
Saltator similis (s)	0.278	0.258	0.250	0.472	1	1	1	1	1	1	1	1	ED	OM
Pitylus fuliginosus	0.042												FM	OM
Volatinia jacarina										1		1	ED	OM
Tiaris fuliginosa	0.028												FU	OM
Sporophila caerulescens			0.028		1		1	1	1		1	1	ED	OM
Sicalis flaveola			0.042	0.014			1		1	1		1	ED	OM
Haplospiza unicolor (s)	0.347	0.419*		0.056									FU	OM
Zonotrichia capensis (s)	0.070	0.210	0.542*	0.481	1	1	1	1	1	1	1	1	ED	OM
Poospiza lateralis (s)	0.014		0.208	0.389	1	1	1	1	1	1			ED	OM
Carduelis magellanicus (s)	0.014	0.032	0.028	0.139	1	1	1	1	1	1		1	ED	OM

[a] Habitat (OA = open area; ED = edge; FU = forest understory; FM = forest mid-levels; FC = forest canopy).
[b] Feeding habit (OM = omnivore; FR = frugivore; NE = nectarivore; CA = carnivore; GI = generalized insectivore; LI = leaf insectivore; TI = trunk insectivore) is shown for each species.

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DO MAMMALIAN NEST PREDATORS FOLLOW HUMAN SCENT TRAILS IN THE SHORTGRASS PRAIRIE?

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ABSTRACT.—Nest predation, the major cause of nest failure in passerines, has exerted a strong influence on the evolution of life history traits of birds. Because human disturbance during nest monitoring may alter predation rates, we investigated whether human scent affected the survival of artificial ground nests in shortgrass prairie. Our experiment consisted of two treatments, one in which there was no attempt to mask human scent along travel routes between artificial nests, and one in which we masked human scent with cow manure, a scent familiar to mammalian predators in the study area. We found no evidence that human scent influenced predation rates, nor that mammalian predators followed human trails between nests. We conclude that scent trails made by investigators do not result in lower nesting success of passerines of the shortgrass prairie where vegetation trampling is minimal, mammalian predators predominate, and avian predators are rare. *Received 9 Nov 1998, accepted 10 Feb. 1999.*

Predation has exerted a strong influence on the evolution of habitat selection and life history traits for many avian species (Martin 1993b). Research on a broad array of ecological topics requires estimates of avian fecundity. Because nest predation is the major cause of nest failure in passerines (Ricklefs 1969; Martin 1992, 1993a, b), researchers have frequently expressed concerns that monitoring might artificially increase predation rates (Mayfield 1975, Major 1990, Gotmark 1992).

Predators might be attracted to nests by visual cues, such as the presence of researchers, trampling of vegetation, increased activity of parent birds, and by olfactory cues. Mammalian predators are thought to follow tracks in the vegetation and to respond to human scent along the trails or at the nests (Creighton 1971, Wilson 1976, Nol and Brooks 1982, Gotmark 1992, Whelan et al. 1994). In a review paper on investigator bias, Gotmark (1992) concluded there was little or no evidence that researcher disturbance increased mammalian predation rates. Of three studies that have directly addressed whether human scent increases mammalian predation rates (Keith 1961, MacIvor et al. 1990, Whelan et al. 1994), one (Whelan et al. 1994) supported the hypothesis. Even though evidence is scant, the use of rubber boots and gloves is widely recommended to alleviate the potential problem of human scent leading to bird nests (Nol and Brooks 1982, Yahner et al.1993, Major and Kendal 1996).

Artificial bird nests have been widely used in predation studies (e.g., Gottfried and Thompson 1978, Yahner and Wright 1985, Yahner et al. 1993). Despite problems with interpretation of results (Major and Kendal 1996), they remain a useful tool for testing predation theories. We conducted an experiment using artificial ground nests in a shortgrass prairie where the primary nest predators are mammals and human presence is rare. Our objective was to test if human scent increased the rates of predation on shortgrass prairie ground nesting birds by comparing two methods of experimenter travel between nests.

The purpose of our study was to determine the most expedient technique for ongoing breeding bird studies in the shortgrass prairie. We do not intend to make inferences from this study to other ecosystems and predator communities. Because breeding systems vary in predator communities, predator behavior, exposure to human presence, vegetation structure, and nest position, many systems need to be evaluated before we can fully understand the effect of human scent on predation rates.

METHODS

We conducted this experiment in July 1997 on Pawnee National Grassland, 7 km northwest of Briggsdale, Weld County, Colorado (40° 41′ N, 104° 24′ W). The 259 ha tract of grazed shortgrass prairie is characterized by short and mid-grasses, cacti (*Opuntia sp.*),

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forbs, and patchy areas of yucca (*Yucca glauca*). Common ground nesting passerines in the vicinity include Horned Lark (*Eremophila alpestris*), Lark Bunting (*Calamospiza melancorys*), McCown's Longspur (*Calcarius mccownii*), Chestnut-collared Longspur (*Calcarius ornatus*), and Western Meadowlark (*Sturnella neglecta*). Potential predators of ground-nesting birds include thirteen-lined ground squirrel (*Spermophilus tridecemlineatus*), deer mouse (*Peromyscus maniculatus*), northern grasshopper mouse (*Onychomys leucogaster*), coyote (*Canis latrans*), swift fox (*Vulpes velox*), raccoon (*Procyon lotor*), long-tailed weasel (*Mustela frenata*), badger (*Taxidea taxus*), striped skunk (*Mephitis mephitis*), and several snake species.

We placed 100 artificial nests along two transects established 800 m apart in similar habitat. Each transect contained 25 lines perpendicular to the transect and alternating in opposite directions at 50 m intervals so that adjacent lines were 100 m apart. Each line contained two nests; one at 100 m (Nest A) and the second at 200 m (Nest B) from the transect. From Nest B we walked an additional 100 m so that both nests on the line were treated equally. To aid in relocating nests we noted any distinguishing features around the nest and tied surveyor's tape to low-growing vegetation 10 m from each nest, a distance not associated with increased predation rates (Major and Kendal 1996).

To test if human scent trails influenced predation rates, we subjected artificial nests to two treatments. In Treatment 1 (human scent), we wore leather boots and made no attempts to mask human scent while walking between nests. In Treatment 2 (masked scent), we masked human scent with a scent familiar to potential predators in the study area by wearing rubber boots that were sprayed with a cow manure tea (fresh cow manure steeped in water, in a 1:3 mixture for at least 12 hours) at the beginning of each line. Treatment types were randomly assigned to the 50 lines (25 lines per transect); both nests on a line received the same treatment. Because we specifically wanted to determine an effect of scent trails, we wore vinyl craft gloves (standard field practice) while handling eggs in both treatments to minimize human scent on the eggs.

Nests consisted of a scrape on the ground and contained two fresh Japanese quail (*Coturnix japonica*) eggs (mean length × width, 3.3 × 2.6 cm, $n = 20$) and one clay egg (2.2 × 1.5 cm, $n = 20$). Scrapes were created using the broad end of a large wooden tongue depressor. While wearing rubber gloves we constructed clay eggs out of soft modeling compound (Sculpey III brand) to approximate the size of Lark Bunting eggs. Clay eggs aided in the identification of nest predators and enabled us to record predation by predators too small to handle quail eggs (i.e., small rodents; Major and Kendal 1996).

Nests were set out on 9 July 1997 and checked three days later, a time interval during which we expected 50% of the nests to survive based on preliminary results of trials using artificial nests constructed in the same manner. Although several studies used longer trial intervals, we expected that our ability to detect differences would be diminished if nearly all nests were depredated. Nests were classified as intact or disturbed based on signs of disturbance to either quail or clay eggs. Nests were considered disturbed if quail eggs were missing, broken, or moved, or if clay eggs were missing, moved, or had tooth impressions. We collected extant clay eggs for examination and identification of any diagnostic marks. We classified markings on the clay eggs as rodent, non-rodent, insect, or unknown by comparing them with known tooth impressions made from skulls in the zoology collection at Colorado State University, Fort Collins, Colorado. In the absence of other signs of disturbance, nests containing clay eggs with only insect marks were considered intact.

TABLE 1. Predation outcomes for 25 lines receiving the human scent treatment and 25 lines receiving the masked scent treatment.

	Predation outcome (1 = depredated, 0 = survived)		Number of lines with outcome	
i	Nest A	Nest B	Human scent (n_i)	Masked scent (m_i)
1	0	0	6	5
2	1	0	5	8
3	0	1	9	7
4	1	1	5	5

The data from this experiment are counts and can be arranged into an $i \times j$ contingency table (Table 1), where i denotes the predation outcome and j denotes the treatment (i.e., human or masked scent). While the cell probabilities for such tables are commonly modeled and estimated using standard loglinear models (e.g., Agresti 1990), reparameterization of the underlying multinomial model can lead to loglinear models that are difficult to construct or difficult to interpret. In this study we reparameterize the underlying multinomial model to address the following specific questions: (1) do predation probabilities differ for nests on a line because of differences in their proximity to the transect, (2) do predation probabilities for nests differ because of differences in human and masked scent treatments, and (3) is there evidence that predators followed the investigator's trail between nests on a line. Hence, instead of using a loglinear modeling approach, we derived parameter estimates and constructed hypothesis tests using classical maximum likelihood methods (e.g., Larsen and Marx 1986:261). The general procedure was to (1) construct the appropriate likelihood function for the data, (2) derive estimators and compute estimates for parameters under the model, (3) evaluate the likelihood function at the maximum likelihood parameter estimates to obtain the deviance (here we omit the term for the saturated model and define deviance as $-2 \times$ (log-likelihood), and then (4) test specific hypotheses using likelihood ratio tests for nested models (Agresti 1990:211). The models used in this study are presented in the Appendix. SAS statis-

TABLE 2. Three candidate models for estimating predation probabilities constructed using (A.1).

Model	Parameters and Constraints	Deviance
1	p_A, p_B, c_A, c_B	137.182
2	$p_A = p_B$, $c_A = c_B$	138.549
3	$p_A = p_B = c_A = c_B$	138.589

tical software (version 6.12 on an IBM-compatible microcomputer; SAS Institute Inc. 1990) was used for all computations. Values reported are means (±SE).

RESULTS

During the trial, 49 of 100 nests were disturbed, 24 from the human scent treatment and 25 from the masked scent treatment. Disturbance to quail eggs was apparent in 45 of 49 (92%) nests; eggs were missing from 12 nests, broken in an additional 7 nests, and moved in an additional 26 nests. In four nests, the quail eggs were undisturbed, yet clay eggs were either moved or had tooth impressions. Clay eggs were undisturbed in only two nests with disturbed (broken) quail eggs. Rodent tooth impressions were identified on 22 clay eggs, and non-rodent impressions on one clay egg. Clay eggs were missing from 20 nests. Quail eggs and clay eggs that were moved were displaced an average of 31.3 cm (± 9.10, median 1 cm, range 0.5–330 cm, $n = 41$) and 43.2 cm (± 15.07, median 20 cm, range 0.5–250 cm, $n = 20$) from their original positions, respectively.

Predation outcomes for the two treatments are summarized in Table 1. In general, few differences between the treatments were evident. In Table 2, the three candidate models constructed under A.1 are presented, along with their deviance. The likelihood ratio test between model 2 and model 1, which tests for differences in predation rates between nest A and nest B caused by their proximity to the transect, had a P-value of 0.505 ($\chi^2 = 1.37$, $df = 2$). Hence, there appears to be no effect as a result of proximity to the transect. The likelihood ratio test between model 3 and model 2, which tests for differences in predation rates caused by differences in the human and masked scent treatments, had a P-value of 0.841 ($\chi^2 = 0.04$, $df = 1$). Hence, we conclude there was no treatment effect.

For the two-parameter model in A.2 (i.e., p, p'), which allows unconditional and conditional predation probabilities for nests on a line to differ, we get a deviance of 97.094. When we impose the constraint $p = p'$ (giving us a one-parameter model that is equivalent to model 3 in Table 2), we get a deviance of 98.387. The likelihood ratio test for these models, which tests whether predators were following the investigator's trail between nests on a line, had a P-value of 0.256 ($\chi^2 = 1.29$, $df = 1$). Consequently, we conclude predators did not follow the investigator's trail between nests on a line.

The one parameter models from A.1 and A.2 are mathematically equivalent and, based on the likelihood ratio tests, are the appropriate models to use for parameter estimation. Hence, the estimated three-day predation probability for nests in this study was 0.49 (±0.050), which gives an estimated daily survival probability of 0.80 (±0.026).

DISCUSSION

We found no evidence that human scent trails to nests altered predation rates on artificial nests in grasslands where the main predators are small mammals, nor did we find evidence that predators were more likely to depredate nests on the same trail. A learned association of human scent with food is unlikely because human presence is rare throughout much of our study area. Rather, the scent would be novel to small mammals of the region. We found no evidence that novel scent was an attractant to predators in our region.

Whether human scent is an attractant or deterrent to predators has been a topic of speculation (Creighton 1971, Mayfield 1975, Wilson 1976, Gotmark 1992) that has been directly tested in only three other studies. Results differ between studies. Keith (1961) reported no effect of human scent on survival of artificial duck nests in wetlands with predominately mammalian predators. MacIvor and coworkers (1990) found that red fox (*Vulpes vulpes*) avoided human scent associated with experimental plover nests along a beach. In contrast, Whelan and coworkers (1994) reported raccoons in a forested system preying on nests with human scent and novel scent more frequently than nests with no scent or familiar scent. In another study evaluating the influence of familiar and novel scents, Clark

and Wobeser (1997) determined that a novel odor (lemon juice and ground ginger root) did not affect survival of artificial waterfowl nests. Collectively, these studies represent a broad variability in predator community composition, predator behavior, exposure to human presence, vegetation structure, and nest placement.

Evidence of other aspects of investigator bias on predation rates is also equivocal. Frequency of nest visits had no effect on predation rates of artificial nests in several studies (Bowen et al. 1976, Gottfried and Thompson 1978, Erikstad et al. 1982, MacIvor et al. 1990, Gotmark 1992, Mankin and Warner 1992), but did in two studies (Major 1990, Esler and Grand 1993), presumably because of vegetation trampling. In our study, we did not evaluate the effects of frequency of visitation nor vegetation trampling. In the shortgrass prairie, the one visit to artificial nests during construction resulted in minimal vegetation trampling.

One criticism of artificial nests is that they often contain only quail eggs and that small predators unable to handle the quail eggs may be under-represented (Major and Kendal 1996). We addressed this problem by considering nests disturbed when eggs were moved as well as broken or removed, and by using smaller clay eggs in addition to quail eggs. We found, however, that only two nests would have been misclassified as undisturbed if only quail eggs had been used.

We conclude that the procedures we used while visiting nests are unlikely to contribute to reduced nesting success of passerines of the shortgrass prairie where vegetation trampling is minimal, mammalian predators predominate, and avian predators are rare. Our conclusion is consistent with Gotmark (1992) who surmises that passerines are less sensitive to investigator disturbance than other groups of birds, scent having less effect than vegetation trampling, and increases in predation in response to human cues more common for avian than mammalian or reptilian predators. We recommend that investigators continue to evaluate whether human scent alters predation rates in avian breeding systems and not make inappropriate inferences across systems. Human scent studies that identify and describe the predator communities, habitat structure, and human influence will ultimately contribute to better understanding of observer bias in research.

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APPENDIX

For a particular line receiving either the human scent or the masked scent treatment, four outcomes are possible (Table 1). If we denote these outcomes by i ($i = 1, \ldots, 4$), let the probability of the i-th outcome be π_i and γ_i (respectively) for human and masked scent treatments, and let n_i and m_i (respectively) be the number of lines for which the i-th outcome was observed for human and masked scent treatments, then the probability of the observed data is the product of two multinomials:

$$C_1 \prod_{i=1}^{4} \pi_i^{n_i} C_2 \prod_{i=1}^{4} \gamma_i^{m_i}$$

where C_1 and C_2 are multinomial coefficients, $\Sigma_i \pi_i = \Sigma_i \gamma_i = 1$, and $\Sigma_i n_i = \Sigma_i m_i = 25$. Under the assumption that lines and nests on a line are independent (the latter assumption is tested below using A.2), we can reparameterize this model in terms of the probability nest A and nest B were depredated for human scent treatments (p_A and p_B) and the probability nest A and nest B were depredated for masked scent treatments (c_A and c_B), to obtain a model with likelihood function proportional to:

$$\begin{aligned}[(1 - p_A)(1 - p_B)]^{n_1}[p_A(1 - p_B)^{n_2}[(1 - p_A)p_B]^{n_3} \\ \times [p_A p_B]^{n_4}[(1 - c_A)(1 - c_B)]^{m_1}[c_A(1 - c_B)]^{m_2} \\ \times [(1 - c_A)c_B]^{m_3}[c_A c_B]^{m_4}. \qquad \text{(A.1)}\end{aligned}$$

We derived estimators for p_A, p_B, c_A, and c_B using standard maximum likelihood methods (Larsen and Marx 1986:261). Differences in predation probabilities between nests A and B due to differences in proximity to the transect, and differences in predation probabilities due to differences in treatments, were tested by constraining parameters in A.1 to obtain the appropriate submodels, and then performing likelihood ratio tests. In the first submodel parameters were constrained so that, within a treatment, predation probabilities for nests A and B were constant (i.e., $p_A = p_B$ and $c_A = c_B$). In the second submodel parameters were constrained so that predation probabilities were constant between nests A and B and across treatments (i.e., $p_A = p_B = c_A = c_B$; see Table 1).

In an effort to determine whether predators were following the human trail between nests, one additional model was constructed. This model assumed that predation probabilities among nests on a line and among treatments did not differ, but allowed the unconditional and conditional predation probabilities of nests on a line to differ. Here, the conditional predation probability is the probability nest A would be depredated given nest B had already been depredated, or the converse. If we denote the unconditional predation probability by p and the conditional predation probability by p', then the probability neither nest on a line is depredated is given by $(1 - p)(1 - p)$ and the probability both nests on a line are depredated is given by pp'. To obtain the probability that only one nest on a line is depredated, we exploit the fact that the cell probabilities for a multinomial must sum to one. Hence, the probability that only one nest on a line is depredated is given by $1 - (1 - p)(1 - p) - pp'$ which, after some algebraic manipulation, yields the intuitively reasonable

$p(1 - p') + (1 - p)p$. Thus, the resulting model has likelihood function proportional to:

$$[(1 - p)(1 - p)]^{(n_1 + m_1)}[p(1 - p') + (1 - p)p]^{(n_2 + n_3 + m_2 + m_3)}[pp']^{(n_4 + m_4)} \quad \text{(A.2)}$$

where n_i and m_i ($i = 1, \ldots, 4$) are as defined above. A test for H_0: $p = p'$ versus H_a: $p \neq p'$ was constructed using a likelihood ratio test.

Short Communications

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Christmas Shearwater Egg Dimensions and Shell Characteristics on Laysan Island, Northwestern Hawaiian Islands

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ABSTRACT.—The mean fresh egg mass of Christmas Shearwaters (*Puffinus nativitatis*) on Laysan Island, in the Northwestern Hawaiian Islands, was 44.9 ± 3.4 (SD) g, and the mean egg volume was 42.3 ± 2.9 cm^3. The measured length and breadth of the eggs, the shell mass, shell thickness, and number of pores in the shell were within 10% of predictions for procellariiform birds, based on fresh egg mass or on both fresh egg mass and incubation period. These data conform with evidence that there are few allometric differences between the eggs of tropical Procellariiformes and those of Procellariiformes from higher latitudes. *Received 19 Oct. 1998, accepted 25 Feb. 1999.*

The Christmas Shearwater (*Puffinus nativitatis*) is a tropical procellariiform seabird that breeds on islands in the central North and South Pacific oceans (Warham 1990). It has been little studied, perhaps because the species is not abundant anywhere (Shallenberger 1984). The purpose of the present note is to report data for Christmas Shearwater eggs collected on Laysan Island (28° 12′ N; 177° 20′ W) in the northwestern Hawaiian Islands.

We measured egg volume by weighing the egg in air and again submerged in water. From the difference between the mass in air and in water, and the density of water, egg volume can be determined in accordance with Archimedes' Principle (Rahn et al. 1976). We determined fresh egg mass by weighing the egg after filling the aircell with distilled water (the mass loss of the egg during incubation being entirely the result of the loss of water vapor; Grant et al. 1982), and we measured both the length and breadth of the egg with a dial caliper. We obtained the shell mass, its thickness, and we counted the number of pores in the shell of randomly-selected sub-samples of eggs after drying the shells in a desiccator. We measured pore density using the procedure described by Tyler (1953) and Roudybush and coworkers (1980).

The mean fresh egg mass of 18 Christmas Shearwater eggs was 44.9 ± 3.4 (SD) g. Knowledge of the fresh egg mass provides an opportunity to compare some of the other measured values (Table 1) with predictions for procellariiform eggs, based on the mass of their freshly laid eggs (Rahn and Whittow 1988). There are no predictive equations for the volume of the eggs of Procellariiformes, but measured egg lengths and breadths were similar (100.3% and 96.0%, respectively) to predicted values (Table 1). Measured shell mass and shell thickness were also similar (94.7% and 105.6%, respectively) to predictions (Table 1). Rahn and Whittow (1988) presented two predictive equations for the total number of pores in the eggshell. Both require the calculation of the surface area of the egg from its mass (Tullett and Board 1977), which is then multiplied by the measured pore density (Table 1). The resulting estimated total number of pores in the shell of a Christmas Shearwater's egg is 3103 pores. This value falls between the two predicted values (2963 and 3584). The predicted values were both based on the incubation period as well as on the fresh egg mass; for this purpose, we used an incubation period of 53 days (Byrd et al. 1983, Naughton 1983) and a fresh egg mass of 44.9 g.

The measured values for the eggs and eggshells of the tropical Christmas Shearwater are close to predictions for Procellariiformes in general. This finding supports evidence that there are few differences in the allometric relationships of eggs and eggshells of Procellariiformes between tropical and non-tropical species. In contrast, there are substantial differences between Procellariiformes and other

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TABLE 1. Measured and predicted values for the eggs and eggshells of Christmas Shearwaters on Laysan Island. The mean measured values (± 1 SD) are shown; n = the numbers of observations. Predicted values are calculated following Rahn and Whittow (1988).

	Measured ($\bar{x}$ ± SD)	n	Predicted
Egg			
Volume (cm^3)	42.3 ± 2.9	19	
Length (cm)	55.6 ± 2.0	22	55.5
Breadth (cm)	38.3 ± 1.3	22	39.9
Eggshell			
Mass (g)	2.9 ± 0.2	8	3.0
Thickness (mm)	0.3 ± 0.0	11	0.3
Pore density [pores $(cm^2)^{-1}$]	59.8 ± 4.7	6	

orders of seabirds in this regard (Whittow 1984, Ar and Rahn 1985).

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The Paint-billed Crake Breeding in Costa Rica

David M. Watson[1,2] and Brett W. Benz[1]

ABSTRACT.—We report a recent observation from southern Costa Rica of the Paint-billed Crake (*Neocrex erythrops*), a little known species from eastern and northern South America. An adult and recently hatched chick were observed at close range in wet grassy second-growth. This observation constitutes the first record of the young of this species and represents the only breeding record for Central America. *Received 12 Nov. 1998, accepted 12 Feb. 1999.*

On 5 June 1998, at 16:30 an adult Paint-billed Crake (*Neocrex erythrops*) was observed, accompanied by a chick, near the

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town of Golfito on the Pacific coast of Costa Rica, close to the Panama border (8° 37′ N, 83° 11′ W). Observations were made by both authors and K. Cohoon, while walking slowly beside the Golfito airstrip amidst grassy second growth interspersed with a row of large *Ficus* trees. Behind this vegetation was a slow moving stream with thickets of tall grass along its banks. We saw the birds from approximately 15 m and watched them for 25 seconds using binoculars. The adult paused in the middle of the path, eventually returning to the wet grassy second growth from which it had walked. The bright yellow bill with a scarlet base, and black and white barred flanks were clearly visible, clearly distinguishing it from the congeneric Colombian Crake (*Neocrex colombianus*). The chick was covered uniformly in black natal down and the tarsi were dark grey or horn. Further soft-part colors were not noted because it quickly ran away from the adult, across the path into thick undergrowth beside the airstrip. Despite subsequent visits to this locality for several weeks, we made no further observations of this species.

Neocrex erythrops is a little known species that ranges widely in eastern and central South America; *N. e. olivascens* is known east of the Andes from Colombia and Venezuela south to Paraguay and Argentina, and *N. e. erythrops* from west of the Andes in coastal Peru and the Galapagos Islands (Ripley 1977). There have been reports of vagrants within South America (Osborne and Beissinger 1979), from suburban areas and up to 3375 m elevation (Remsen and Traylor 1983), and some recent reports (Tostain et al 1992, Haverschmidt and Mees 1994) suggest that the species may be resident in Surinam and French Guyana. As with many other species of rail, the chicks of this species are undescribed (Ripley 1977, del Hoyo et al 1996). The uniform black down and dark tarsi are similar to the young of other neotropical rails in the genera *Laterallus* and *Porzana*.

The status of this species in Central America is unclear. There is only one definite record from Costa Rica, from the Sarapiquí lowlands in the northeast by Stiles and Rosselli on 22 August 1987 (Stiles and Skutch 1989). There is an additional record of either this species or the similar *N. colombianus* from southern Costa Rica, near Hitoy Cerere in March 1985 (Pratt et al., reported in Stiles and Skutch 1989). Two specimens collected in the coastal lowlands of Bocas del Toro, Panama on 10 November 1981, were later identified by Ripley as the wide-ranging *N. erythrops olivascens*; several individuals were seen at Tocumen Marsh in eastern Panama by Behrstock (1983). All of these records are from the Caribbean lowlands, thus the record reported herein constitutes the first for the Pacific slope of Central America.

There are two records from North America: from east central Texas on 17 February 1972 (Arnold 1978), and Virginia on 15 December 1978 (Blem 1980). Both these records were probably wandering individuals, a pattern seen in many other species of rail (Remsen and Parker 1990). In contrast to these winter records, the two records from Costa Rica are from August and March. Based on the June 15 record we report, and the clear evidence of breeding, we suggest that *N. erythrops* has a breeding population in southern Costa Rica.

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Additional Records of Fall and Winter Nesting by Killdeer in Southern United States

Kimberly G. Smith,[1,6] W. Marvin Davis,[2] Thomas E. Kienzle,[3] William Post,[4] and Robert W. Chinn[5]

ABSTRACT.—We report on successful nesting attempts in fall by Killdeer (*Charadrius vociferus*) in southern Mississippi in November, 1987 and in central Arkansas in October, 1998, and a winter nesting attempt in South Carolina in December, 1998. The first nest was found 1 year before previously reported fall nestings in the Southeast and 1 month earlier in the season. The second is the most northern and western fall nesting site in the South, and the third is the latest reported nesting attempt in the southern United States. Taken together with 3 other reported successful fall nests in Mississippi and South Carolina, Killdeer would appear to be the only fall breeding shorebird in North America and, based on those 6 widely-scattered observations over the last 11 years, should now be considered a rare fall and winter breeder across the southern United States. *Received 24 Nov. 1998, accepted 31 March 1999.*

Although an anomalous report of breeding in November exists from Michigan in 1982 (Tessen 1983), Jackson and coworkers (1995) were the first to document fall and winter breeding by Killdeer (*Charadrius vociferus*) in the southeastern United States, reporting 1 set of chicks and adults on 16 November and another set on 11 December 1988 in Okibbeha Co., Mississippi. Subsequently, Post (1996) reported 3 downy young, apparently 1–2 days old, taken to a veterinarian in Berkeley Co., South Carolina on 13 November 1995. Here we report on two more successful fall nesting attempts by Killdeer in the south: one from Mississippi that is earlier than observations by Jackson and coworkers (1995), and one from central Arkansas, the most northern and western fall nesting site yet reported in the South. We also document a mid-December winter nesting attempt in South Carolina, which is the latest nesting activity yet reported.

On 7 November 1987, W.M.D. found and photographed a pair of adults with one chick, which appeared to be several days old, at the wastewater treatment plant lagoon in Waveland, Hancock Co., coastal Mississippi. The race-track shaped lagoon was surrounded by a 4.5–9.2 m raised strip of excavated soil, which varied from well-grassed to almost bare areas, one of which was evidently chosen for nesting by the Killdeer.

On 5 October 1998, T.E.K. and his wife discovered a nest with four eggs located in a stone area on the barrier of the parking lot at the Veterans Administration Hospital in Little Rock, Pulaski Co., Arkansas. During daily observations, two birds were usually present and the female was observed incubating during the day. They found two chicks on 26 October and a third on 28 October. The nest was aban-

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doned with one egg remaining on 29 October. Subsequent analysis determined that the egg was fertile, but did not hatch.

On 5 December 1998, R.W.C. found a Killdeer nest containing four eggs in North Charleston, Charleston Co., South Carolina. The nest was a shallow depression located on an approximately 0.2 ha lawn covered with short (2–3 cm) grass. The nest was about 10 m from a frequently traveled road in a U.S. Post Office complex. He made repeated visits to the site, and found adults incubating daily during 5–15 December. On 16 December, after arrival of a cold front on the coast, no Killdeer were seen in the area, and Chinn concluded that the adults had abandoned the nest. On 17 December at 15:00 EST, W.P. checked the area, and finding no Killdeer, collected the four eggs (ChM # 1998.11.50a–d), which were intact but cold. The heaviest egg weighed 11.7 g; the lightest, 10.8 g. Dimensions of the longest egg were 40.2 × 25.6 mm; the shortest, 37.9 × 26.5 mm. No egg had a discernible embryo, although the contents of all appeared to be fresh.

Killdeer would appear to be the only fall nesting shorebird in North America. There are apparently no records of Killdeer breeding in Mexico (P. Escalante, A. T. Peterson, pers. comm.), and no evidence of breeding later than July in southern California based on clutches in the collection at the Western Foundation of Vertebrate Zoology (M. Marin, pers. comm.). However, based on breeding records from October, February, May, and August, Robertson (1962) concluded that Killdeer breed throughout the year in the Caribbean. Schardien (1981) determined that Killdeer have year-round territories in Mississippi and copulations have been observed during winter months (Jackson and Jackson, in press). Thus, those six widely scattered records of breeding over the last 11 years would suggest that the Killdeer should now be considered a rare fall and winter breeder in southern United States.

Incidental fall breeding in temperate regions has been documented for a wide variety of birds (e.g., Orians 1960), but repeated fall (or winter) breeding seems to be triggered by either an appropriate stimulus appearing naturally, e.g., green cones stimulating breeding in Pinyon Jays (*Gymnorhinus cyanocephalus*; Ligon 1978), or an appropriate stimulus occurring during the wrong season, e.g., Tricolored Blackbirds (*Agelaius tricolor*) breeding in fall in response to flooding of rice fields (Orians 1960). Those recent observations of fall breeding by Killdeer could be due to a combination of events, including more birdwatchers being active during fall and early winter in areas of the South than in previous times. However, the most likely explanation is the unusually warm years that have occurred over the last decade or so (Mann et al. 1998). Jackson and coworkers (1995) noted that their observations followed a summer drought and mild fall weather, which is similar to the situation in Arkansas during 1998. The period from May through September of 1998 was the hottest on record at Little Rock, with 18 days above 37.8° C, 59 days above 35° C, and 111 days above 32.2° C and below average rainfall (National Weather Service, North Little Rock, Arkansas). Warm fall weather may be extending the breeding season into fall, and even winter, months, but there are apparently few, if any, breeding attempts reported for late August and September. More likely, extended warm fall weather stimulates Killdeer to resume breeding, as they typically are very early spring breeders in the south [e.g., nests found in February of 1999 in Louisiana (W. M. D.)].

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Wild Turkeys (*Meleagris gallopavo*) Renest After Successful Hatch

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ABSTRACT.—Wild Turkey (*Meleagris gallopavo*) hens frequently renest after disturbance on the nest, especially while laying or early during the incubation period. However, no record exists of Wild Turkey hens renesting after a successful hatch. We document three Wild Turkey hens that renested after having hatched a brood. None of the renests were successful. *Received 2 Dec. 1998, accepted 6 March 1999.*

Nesting success of Wild Turkeys (*Meleagris gallopavo*) varies widely across their range and is influenced by many factors (Vangilder 1992). A successful nest generally is defined as one in which at least one poult hatches. Researchers have documented many instances of Wild Turkey hens renesting after their initial nest was disturbed or depredated (Everette et al. 1980, Williams et al. 1980, Vangilder et al. 1987), most often while laying or during early incubation (Williams et al. 1976). Causes for nest failure and subsequent renesting include nest destruction by predators (Speake 1980, Vander-Haegen et al. 1988), severe weather (Roberts and Porter 1998, Kimmel and Zwank 1985), and disturbance by researchers (Still and Baumann 1990). Renesting after a successful nest was not thought to occur. In his *Book of the Wild Turkey*, Williams (1981:53) stated, "No example is known of a hen nesting again in the same year after her brood hatched, and there has been no reported case of a turkey hatching two broods in one year." Below, we document three cases of hens renesting after having successfully nested but with early loss of broods.

In 1983, while working in southern Alabama, J.H.E. found a Wild Turkey hen that renested three times after hatching a brood that did not survive more than two days. This particular hen hatched all 11 eggs in her initial clutch after a normal incubation period (28 days). On the day after hatching, five of the poults were found dead in the nest from unknown causes. The hen had no poults with her two days after hatching, and the fate of the remaining six poults was never determined. Twenty-five days after hatching, the hen renested. This nest was disturbed by investigators, which prompted the hen to abandon that nest and eventually renest two more times. None of the renests was successful.

In the southern Appalachians of North Carolina, C.A.H. monitored two wild turkey hens that renested after hatching clutches of 11 and 14 eggs. These nests were initiated in early April of 1996, and incubated 29 and 27 days. Both broods were killed within five days. One hen initiated a second nest 17 days after her initial clutch hatched. This renest contained nine eggs that were incubated 65 days, 37 days beyond the normal 28-day incubation period. Subsequently, this nest was abandoned, and the eggs were determined to be infertile.

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The second hen began incubating another nest 27 days after her initial clutch hatched. This renest was incubated for 11 days and abandoned for unknown reasons.

None of the renests we documented was successful, either because of infertility or nest abandonment. Ultimately, infertility could be a primary factor limiting success of late renests. Sperm may be contained in a hen's oviduct up to 56 days after copulation (Blankenship 1992) and remain viable for a 'normal' renesting attempt. However, the renests we documented were initiated considerably later than most renests because they occurred after an entire incubation period plus some additional days. Thus, a hen might need to copulate again in order to lay fertile eggs two months after the primary mating season (i.e., April–May). However, copulation in July would be exceptional because the urge to breed, which is associated with the rise in testosterone (for males) and prolactin (for females) levels, is regressing (Blankenship 1992).

The ability of Wild Turkey hens to renest after having hatched a brood did not contribute to productivity in these cases. However, we now know it is possible for hens to renest after a successful nesting attempt and it is conceivable that such nesting could be successful.

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Post-migration Weight Gain of Swainson's Hawks in Argentina

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ABSTRACT.—Swainson's Hawks (*Buteo swainsoni*; Aguilucho Langostero) were captured and banded in La Pampa, Argentina from 28 November 1996 through 25 January 1997. We collected morphometric measurements to determine if hawks gained weight on the austral (non-breeding) grounds. Hawks in apparently healthy condition weighed 819.7 ± 11.1 g (mean ± SE, n = 127, range 540–1090 g). Weight increased significantly over the length of the non-breeding season in Argentina (P = 0.0059), but wingspan (124.9 ± 0.5 cm, n = 127, range 105.7–137.1 cm) and tail (19.8 ± 0.1 cm, n = 127, range 16.5–23.1 cm) did not. When separated by age, weight increased significantly for juveniles (P = 0.0083) but was marginally non-significant for adults (P = 0.0555). *Received 15 Oct. 1998, accepted 15 Feb. 1999.*

Swainson's Hawks (*Buteo swainsoni*) are long-distance migrants that travel between the plains, shrublands, and pampas (grasslands) of North and South America. During the southward migration, some hawks temporarily stop in Central America or in the agricultural zones of Mexico (Ridgely and Gwynne 1989, Stiles and Skutch 1989, Howell and Webb 1995). Occasionally some hawks are found in Florida (Robertson and Woolfenden 1992) and others winter in California (Herzog 1996). The pampas of Argentina are a major non-breeding (austral) destination, supporting much of this species' population from mid-November through early March. Two satellite radiotagged hawks trapped by Brian Woodbridge in California in 1994 were tracked to La Pampa province, Argentina (Woodbridge et al. 1995). Large numbers of hawks were subsequently found in La Pampa, Buenos Aires, and Cordoba provinces (Goldstein et al. 1996).

Adults feed primarily vertebrates to nestlings (England et al. 1997). Summer flocks of non-breeding birds eat a more varied diet, including insects (Johnson et al. 1987). On the non-breeding grounds, hawks are generally seen in large aggregations: roosting, foraging, and traveling together. In the pampas, the hawks primarily eat invertebrates (White et al. 1989, Jaramillo 1993, Woodbridge et al. 1995, Goldstein et al. 1996). The dietary shift allows for more birds to be supported per unit area. In La Pampa, flocks of birds following grasshopper (Orthoptera) outbreaks have been reported (Rudolph and Fisher 1993). We found flocks as large as 12,000 birds (Goldstein 1997).

Long-distance migration using only stored fat has been suspected but not documented (Smith et al. 1986). Whether hawks forage or fast en route to Argentina, or whether specific stopover habitats are regularly used is not known (Goldstein and Smith 1991, Kirkley 1991). The extent of predation on airborn dragonflies and other flying insects during migration is also unknown. Nevertheless, if migrating hawks used only stored fat they might arrive in the pampas in poor condition (Smith et al. 1986). Hawks have been reported arriving in Argentina in such weak condition that they were picked up by hand (C. C. Olrog in Smith 1980). None of these birds, however, were checked for contaminants.

Swainson's Hawks are found in Argentina from early November through mid-February, although later arrivals and earlier departures have been documented (England et al. 1997). Substantial periods of fasting during migration would result in a substantial loss of weight, weakened condition, and a subsequent increase in weight when on the wintering grounds. From November 1996 through January 1997, we captured and measured Swainson's Hawks on the non-breeding grounds. We

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present these data and observations regarding Swainson's Hawk austral weight gain.

METHODS

The research area in northern La Pampa (35° 14′ S, 63° 57′ W, 149 m ASL) is a flat grassland dominated by row crop agriculture. One hundred and twenty-eight Swainson's Hawks were captured and sampled in La Pampa from 28 November 1996 through 25 January 1997. Most hawks were trapped by bal chatri traps in open fields or on dirt roads between foraging fields (Bloom 1987). Nine of the 128 hawks were captured by hand after they were grounded from their nighttime *Eucalyptus viminalis* roost by a thunderstorm. All hawks were captured in the morning between 05:15 and 11:00 local time.

Hawks were banded and weighed to the nearest gram with a 1500 g Pesola scale. Wingspan and tail length were recorded to the nearest mm. Hawks were classified as juveniles or adults based on plumage, with immatures grouped as juveniles (Wheeler and Clark 1995). A regression analysis was used to analyze changes in weight, wingspan, and tail length for the population and for each age category. Time was expressed in number of trap days from Day 1 (28 November 1996). Because sexes could not be distinguished morphologically, we did not analyze the data by sex (Wheeler and Clark 1995). Statistical analyses were performed using SPSS 8.0 for Windows (SPSS Inc., Chicago, Illinois).

RESULTS

We collected complete data sets for 127 healthy hawks. One individual that might have been exposed to pesticides was excluded (Goldstein 1997). Weight averaged 819.7 g [± 11.1 (SE), range 540–1090 g]. Wingspan measured 124.9 cm (± 0.5, range 105.7–137.1 cm), and tail length measured 19.8 cm (± 0.1, range 16.5–23.1 cm). Regression analysis indicated that weight increased significantly over time ($R^2 = 0.0705$, $P = 0.0059$), but neither wingspan ($R^2 = 0.0001$, $P > 0.05$) nor tail length ($R^2 = 0.0078$, $P > 0.05$) increased during the season. This pattern suggested an increase in mass from late November until late January without structural growth.

There were 65 adult, 58 juvenile, and 4 unknown aged birds. Adults weighed 836.6 g (± 16.5, range 560–1090 g). Juveniles weighed 794.2 g (± 15.9, range 540–1080 g). Weight significantly increased over time for juveniles ($P = 0.0083$, df = 57, $R^2 = 0.1179$; Fig. 1A), but was marginally non-significant for adults ($P = 0.0555$, df = 64, $R^2 = 0.0570$; Fig. 1B). Although both age categories showed weight gains, the larger slope for juveniles indicated they gained weight at a faster rate than adults. When examined by age, neither wingspan nor tail length changed over time ($P > 0.05$ for all).

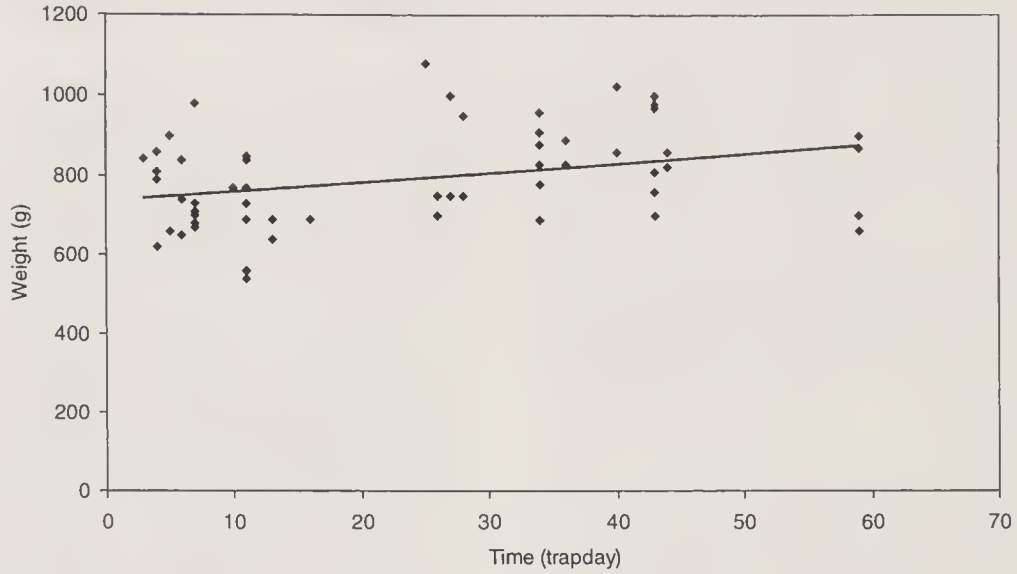
Wingspan was significantly and positively correlated with tail length ($r = 0.509$; $P < 0.05$) and with weight ($r = 0.342$; $P < 0.05$). Weight and tail length showed no correlation ($r = -0.048$; $P > 0.05$).

DISCUSSION

Swainson's Hawks remain in Argentina from mid-November through mid-February (Houston and Schmutz 1995, England et al. 1997). When we began following large flocks on 20 November 1996 we saw no signs of birds in poor condition. Whether birds arrived in Argentina in poor condition is uncertain, but neither our observations nor conversations with farmers supported that conjecture. Although hawks were not in poor condition when captured in late November, they were somewhat lighter than those measured on the breeding grounds. Breeding males weighed 808 g (range 693–936 g, $n = 69$) and females weighed 1109 g (range 937–1367 g, $n = 50$), for an overall mean of 934 g (J. K. Schmutz in England et al. 1997). Although hawks captured in Argentina averaged 819.7 g, birds captured on 28 November–17 December 1996 were notably lighter (779.1 g) than the mean. Hawks captured from Days 21–59 weighed 860.5 g. Both adults and juveniles, when examined separately, show similar patterns of weight for Days 1–20 (adults 814.8 g, juveniles 737.0 g) and Days 21–59 (adults 872.5 g, juveniles 847.7 g). This pattern suggests that both adult and juvenile hawks lost weight during migration and then regained it during their stay in Argentina, although the trend for juveniles was stronger. However, if the hawks foraged in the northern pampas for several days or weeks prior to their arrival near the La Pampa field sites, our measure of weight loss is underestimated.

Rectrix lengths were consistent with those reported from North America (England et al. 1997). Alberta males averaged 18.4 cm (range 17.0–19.8 cm, $n = 61$) and females averaged 20.5 cm (range 19.3–22.1 cm, $n = 43$) for an overall length of 19.3 cm (J. K. Schmutz in England et al. 1997). We found no wingspan

A.



B.

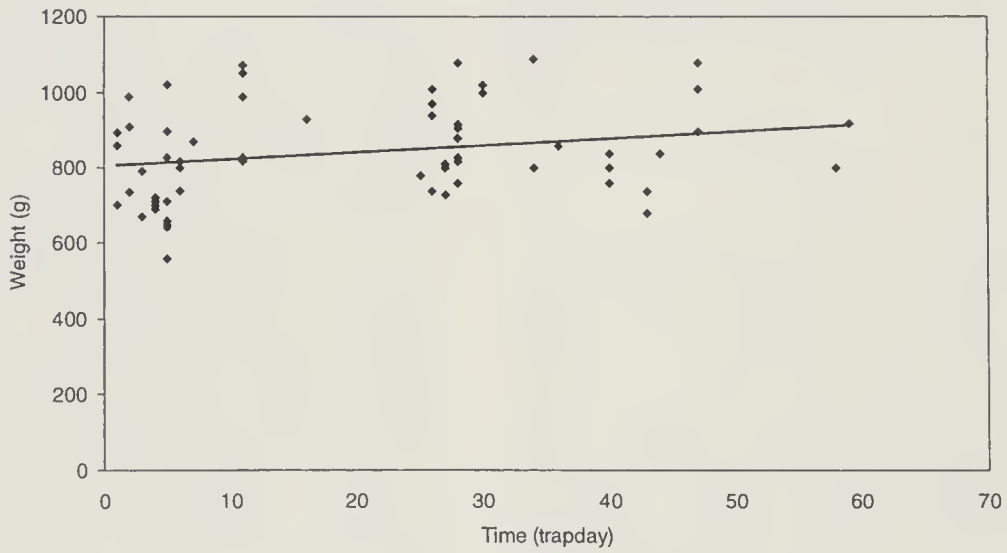


FIG. 1. Swainson's Hawk juvenile (A) and adult (B) austral weights from 28 November 1996 through 25 January 1997 as measured in northern La Pampa, Argentina. Juvenile weight gain was significant ($Y = 2.3972x + 736.65$, $R^2 = 0.1179$, $n = 58$, $P = 0.0083$). Adult weight gain was marginally non-significant ($Y = 1.8196x + 806.89$, $R^2 = 0.0570$, $n = 65$, $P = 0.0555$).

data for North American hawks in the literature. In addition, hawks were molting throughout the non-breeding season in Argentina, a phenomenon that has not been studied.

We captured only one hawk that was light weight and appeared weak. The hawk weighed 560 g when trapped on 25 November 1996. It gained 100 g in 5 days of captivity and was subsequently released. Whether this bird was weak from migration or had been exposed to toxins is unknown. Although no chemical residues were found on either footwash or feather residue samples, cholinesterase measurements from blood plasma samples taken at the time of capture were 30% below those taken at the time of release (Goldstein 1997). Exposure to organophosphate insecticides decreases plasma cholinesterase activity levels (Hill and Fleming 1982).

Large flocks foraging on the ground during

migration were thought unlikely in the past (Smith et al. 1986), but such behavior may not be uncommon (see England et al. 1997, Goldstein 1997). Insect outbreaks in agricultural grasslands may provide terrestrial foraging opportunities along the migration corridor. Recently discovered populations wintering in southwestern Mexico confirm the need for further study of stopover habitats. In addition, hawks are known to forage aerially for grasshoppers and dragonflies across the pampas of Argentina (White et al. 1989, Jaramillo 1993, Rudolph and Fisher 1993, Woodbridge et al. 1995, Goldstein 1997). We have no idea what altitudes are reached while traveling on thermal air currents across the insect-rich tropical and sub-tropical rainforests, nor whether any appreciable distance is ever achieved without aid of thermals. We do not know whether aerial insects are in adequate supply at the heights of travel. The question of the duration and extent of fasting of Swainson's Hawks during migration needs further study although lengthy periods of fasting seem unlikely given the weights of November birds captured in Argentina.

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Siblicide at Northern Goshawk Nests: Does Food Play a Role?

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ABSTRACT.—Siblicide as a mechanism for brood reduction has been reported in a number of asynchronously hatching bird species. Although researchers have documented the occurrence of facultative siblicide in several raptor species, its cause is still debated. Most hypotheses relate incidences of siblicide to food availability. The food-amount hypothesis predicts a negative relationship between the amount of food available and nestling aggression. While the food-amount hypothesis has received much attention, few studies show more than correlational support for this activity in raptors. Our observation of a siblicide event at a Northern Goshawk (*Accipiter gentilis*) nest used as a control in a supplemental feeding experiment, and a similar incident where a nestling goshawk's death can be attributed to siblicide provide support for the negative correlation between food amount and sibling aggression. These observations and the lack of any reported sibling aggression at seven supplementally fed nests showing extreme hatching asynchrony also indicate a relationship between food resources and brood reduction. Our observations are consistent with the idea that goshawks exhibit facultative siblicide, and that resource levels as predicted by the food-amount hypothesis directly influence it. *Received 7 Oct. 1998, accepted 16 Feb. 1999.*

Hatching asynchrony in birds facilitates brood reduction because the last hatched nestling is at a competitive disadvantage if resources provided by the parents prove inadequate. In asynchronously hatched broods, the youngest nestling occasionally dies from aggressive sibling behavior including pecking, exclusion during feeding bouts, or eviction from the nest (Lack 1954, Mock et al. 1990, Creighton and Schnell 1996). Asynchronous hatching results in adapting a brood size to an unpredictable food supply by allowing all young to survive when food is plentiful, but ensuring brood reduction to match parental provisioning capabilities when prey levels are meager (Lack 1954, Newton 1979, Bryant and Tatner 1990, Heeb 1994). Species in which the frequency of siblicide events are variable are termed facultative, while those in which siblicide occurs in nearly all nest attempts are called obligate (Edwards and Collopy 1983). Although the occurrence of obligate siblicide appears to be largely innate (Mock et al. 1990, Gerhardt et al. 1997), the causes of facultative siblicide are still debated (Forbes and Mock 1994).

Fatal sibling aggression has been documented in a range of avian species (Stinson 1979, Braun and Hunt 1983, Anderson 1989, Drummond and Garcia Chavelas 1989, Bryant and Tatner 1990, Mock et al. 1990; Mock and Lamey 1991, Heinsohn 1995, Reynolds 1996). However, an understanding of the proximate factors that influence the occurrence of facultative siblicide remains elusive because such events are rare and unpredictable. Most similar hypotheses attempt to explain facultative siblicide in relation to food.

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The food-amount hypothesis predicts a negative relationship between the amount of food available and nestling aggression (Mock et al. 1987, Creighton and Schnell 1996). By killing its sibling when food is scarce, a nestling may increase its chance of survival by increasing its share of food delivered to the nest. Mock and coworkers (1990) found that smaller food morsels can be monopolized through combat and, therefore, reward sibling aggression. Higher rates of aggression were observed in larger broods of Cattle Egrets (*Bubulcus ibis*) where individual food portions are expected to be smaller (Mock et al. 1987).

Because siblicide events are uncommon, and tend to go unwitnessed unless nests are under constant watch, few studies have established a causal link between food resources and fatal sibling aggression (but see Mock et al. 1987). Facultative siblicide has been documented in several raptor species, but its cause has not been fully investigated (Schnell 1958, Pilz and Seibert 1978, Newton 1979, Bechard 1983, Zachel 1985, Bortolotti et al. 1991, Boal and Bacorn 1994). Although the hypothesis that food supplies influence sibling aggression is intuitively appealing, few studies, with the exception of Wiebe and Bortolotti (1995) and Wellicome (1997), have provided more than correlational support for this activity in raptors.

Northern Goshawks (*Accipiter gentilis*) hatch asynchronously and exhibit siblicide (Newton 1979, Stinson 1979). Observational accounts of siblicide in goshawks are rare (Schnell 1958, Zachel 1985, Boal and Bacorn 1994), and its occurrence is thought to be limited to times when food is in very low supply (Newton 1979). Experimental data linking food resources and incidence of siblicide in this species are nonexistent. In this paper, we report the occurrence of a siblicide event at a goshawk nest in northeastern Utah. We also describe another incident in which a nestling's death was likely the result of siblicide and we provide experimental evidence that the incidence of sibling aggression may be related to food supplies. Our observations are consistent with the hypothesis that goshawks exhibit facultative siblicide directly influenced by food resources.

Our siblicide observations occurred at nests that were part of a study on the influence of food provisioning on female nest attendance and nestling begging vocalizations. This investigation was part of a larger experiment examining the influence of supplemental food on parental care strategies and juvenile survival (Dewey 1999). In 1997, 14 nests were included in the food supplementation experiment (experimental design similar to that of Ward and Kennedy 1996). Seven of these nests were randomly assigned as treatments and were provided Japanese Quail (*Coturnix coturnix*) from hatching through the fledgling dependency period. We visited treatment nests every two to three days and provided sufficient food to meet the energy requirements of the female and young until the next scheduled visit (see Dewey 1999 for details). Control nests were visited at the same interval and for the same amount of time, but were not given food. The nest attendance/vocalization study was conducted from mid-June to mid-July 1997 and consisted of a subset of the nests used in the food supplementation experiment. Each nest was observed for a 3 h period on three different occasions from a portable blind located approximately 30 m from the nest. Observation times were rotated to include both mornings and afternoons.

The first event was witnessed during a 3 h observation period on the afternoon of 10 July at control nest LGD. The adult female had not been observed in the nest stand since 8 July, and likely had deserted the nest or died. Although we were unable to trap the female to verify her age prior to her disappearance, her unusually dark maroon colored eyes, behavior, and degree of scarring above and around her right eye indicated old age. The role of the male in caring for the nestlings after the female's disappearance is unknown because he was never observed visiting the nest.

Shortly after observations had begun, two nestlings (21 and 22 days old) were begging periodically. The older nestling (N1) then began flapping its wings and pecking at the head of nestling 2 (N2). Nestling 2 initially retaliated by flapping its wings and pecking at the head of N1, but soon turned its back to N1 and assumed the defense stance described by Schnell (1958), with its head lowered and its rump elevated. Nestling 1 responded by increasing its intensity of pecking and then began pulling down out of N2's thighs and

rump. Nestling 2 uttered a high-pitched call and moved toward the edge of the nest. This behavior continued as N2 was forced out of the west side of the nest and onto the nest branch. Nestling 1 perched on the edge of the nest and continued pulling down from N2's rump until N2 moved out of reach, at which point N1 walked to the center of the nest and rested.

After approximately 15 min, during which several strong gusts of wind nearly blew N2 off the branch, N2 moved back into the nest; N1 resumed aggressive attacks within 5 min. Nestling 2 again assumed a defense stance, and N1 began tearing down from N2's backside, forcing N2 onto the south edge of the nest. Nestling 1 then began rushing at N2 and colliding with N2's hind end. This behavior continued while N2 called and flapped its wings in an attempt to maintain balance as it clung to the rim of the nest. Nestling 2 then turned quickly and climbed over N1 and into the center of the nest. Nestling 1 pursued N2 to the east edge of the nest next to the tree trunk, where N2 again took a defense stance. Nestling 1 resumed ramming and tearing down from N2. Nestling 2 was knocked out of the nest but caught its wing on a branch. Nestling 1 leaned out of the nest and continued to rip down from N2 while N2 screamed. Nestling 1 then backed off, uttered an adult-like alarm call, and returned to the center of the nest. Nestling 2 climbed back into the nest and remained in the nest for approximately 10 min until N1 again chased N2 out of the nest and onto the nest branch. Nestling 2 was not allowed back onto the nest for the rest of the observation period.

Two days later we found N2 dead on the ground under the nest. Nestling 1 directed loud alarm and begging calls at us throughout the visit to the nest stand. Nestling 1 was found dead in the nest on 14 July 1997. Bodies of both nestlings were sent to the Colorado Veterinary Diagnostic Laboratory at the College of Veterinary Medicine, Colorado State University, where necropsies were performed. Nestling 2 was mildly emaciated, had two fractured ribs, and pulmonary hemorrhaging, presumably incurred during its fall from the nest tree. The exact cause of death for N1 was unknown; however, the necropsy showed this bird suffered from advanced emaciation resulting in pectoral muscle atrophy, which strongly suggests starvation.

The other probable case of siblicide occurred at the control nest SNK on 2 July 1997. When we entered the nest stand the female was not in the immediate vicinity. Two nestlings (20 and 22 days old) were in the nest; one was obviously dead with blood around its head. The adult female returned shortly thereafter, poked at the dead nestling briefly, and then carried the body away from the nest. She returned within several minutes without the dead nestling. Although we did not witness aggression between the siblings, the fact that the dead nestling was still in the nest suggests that a predator did not kill it. Because of the obvious head injury, we believe the nestling's death resulted from siblicide and not merely starvation. Although, it is possible that the remaining nestling attempted cannibalism after its sibling had died, we did not observe the nestling trying to feed on its dead sibling. The SNK nestling's death could also have been the result of filial infanticide if parental behavior (e.g., nest desertion, favoritism, or aggression) contributed to its death (Mock and Parker 1997). However, O'Connor's (1978) brood reduction model predicts that conditions favorable to siblicide will occur more often than those favorable to filial infanticide. To our knowledge, filial infanticide resulting from fatal parental aggression has not been documented in goshawks; nevertheless, we cannot rule it out as a possibility.

Several details of these observations differed from those of similar events observed in goshawks and other raptors. Cannibalism was documented to have followed siblicide in a Swainson's Hawk (*Buteo swainsoni*) nest (Pilz and Seibert 1978), three Burrowing Owl (*Athene cunicularia*) nests (Wellicome 1997), four American Kestrel (*Falco sparverius*) nests (Bortolotti et al. 1991), and three goshawk nests (Schnell 1958, Zachel 1985, Boal and Bacorn 1994). However, cannibalism was not observed at either nest in this study. At the LGD nest cannibalism might have occurred if N2 had not fallen to its death; but N1's behavior gave no indication that it was attacking N2 for the purpose of consumption. Nestling 1 seemed intent on expelling N2 from the nest and N1's aggression stopped once N2 was out of the nest. If N1 was at-

tempting to kill N2 for consumption we would have expected the aggression to continue until N2 was dead. Cannibalism was also not observed at the SNK nest but this may have been due to the presence of the adults that were providing food to the remaining nestling, or to the removal of the dead nestling before it could be cannibalized.

A second disparity between our observations and those in the literature is the potential function of the submissive posture of the defense stance. According to Schnell's (1958) observations of nestling aggression, the aggressor terminated attacks when its sibling assumed the defense stance. In our observations, N1 continued aggressive attacks after N2 assumed the defense stance. Nestling 1's behavior also differed from aggressor behavior in other documented siblicide events in that N1's attacks were aimed primarily at N2's rump and thighs instead of at its sibling's head (Schnell 1958, Pilz and Seibert 1978, Boal and Bacorn 1994).

Although our LGD siblicide observation differs in the aforementioned ways from those previously reported by Schnell (1958), Zachel (1985), and Boal and Bacorn (1994), our event is similar in that it occurred during a period of apparent low food supply. We did not measure food availability in our study area, but provided half of our experimental goshawks with supplemental food. Including the LGD nest failure and the SNK mortality, we documented brood reductions at four of the seven control nests in 1997 and no nestling deaths at any of the treatment nests. Three of the seven (43%) control nests failed (i.e., fledged no young). In addition, the youngest nestling at one supplemented nest hatched 10 days after its closest sibling (mean age difference between oldest sibling and each of the younger siblings = 2.12 days) and was noticeably smaller than its two nest mates, yet survived to fledging age with little aggression between siblings. Ward and Kennedy (1996, unpubl. data) documented similar results in their experiment, where a nest with supplemental food successfully fledged four young including a nestling 7–10 days younger than its closest sibling. Because nestlings that hatch significantly later than their siblings in asynchronous broods often die unless enough food is provided (Bryant and Tatner 1990, Wiebe and Bortolotti 1995), we attribute the higher survival of these treatment nestlings to the high food abundance.

Although our study was not designed to investigate the role of food in sibling aggression in goshawks, our finding of higher survival for supplementally fed nestlings, coupled with the siblicide observations provided us with the opportunity to consider this relationship. Lack (1954) hypothesized that asynchronous hatching in avian species occurs to facilitate brood size reduction to match available levels of resources provided by parents. If Lack's hypothesis is correct, occurrences of siblicide should be influenced by levels of prey abundance. Forbes and Mock (1994) differentiate two types of facultative siblicide: one in which aggression is triggered by food shortage and the other where it is not. Mock and coworkers (1987) observed that the occurrence of fatal sibling aggression in some species was only indirectly influenced by food. They observed aggressive behavior between siblings regardless of food levels, but mortality from aggression was lower if food was abundant because the younger siblings were sufficiently strong to withstand the attacks. Our observations are consistent with the form of facultative siblicide directly influenced by resource levels and provides evidence for the hypothesis that low food supplies trigger sibling aggression in goshawks. Additional empirical research, coupled with measurement of background resource levels is needed to further substantiate this assertion and clarify the nature of the relationship.

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Cooperative Foraging in the Mountain Caracara in Peru

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ABSTRACT.—Cooperative foraging behavior is rarely observed in ground-walking birds. I report on observations of cooperative foraging behavior by Mountain Caracaras (*Phalcoboenus megalopterus*) in the puna region of Peru in September of 1995. On several occasions, three individuals (two adults and one immature) were observed working together to turn over large rocks to obtain prey from beneath. These cooperative foraging events are notable in that, unlike cooperative foraging behavior observed in other ground-walking birds, only one individual obtained prey from a given cooperative effort. The presence of the immature individual may be indicative of delayed dispersal, a behavior not previously described for this poorly known species. *Received 14 Dec. 1998, accepted 28 March 1999.*

Cooperative foraging involves two or more individual organisms assisting one another in obtaining a food item. Among vertebrates, this behavior is well described in many social mammals (Macdonald 1983, Serfass 1995) and some fish (Dugatkin and Mesterton-Gibbons 1996) but is relatively uncommon in birds (Sullivan 1984). Among birds, cooperative hunting appears most frequently in seabirds (Parasitic Jaegers, *Stercorarius parasiticus,* Pruett-Jones 1980; Brown and American White pelicans, *Pelecanus occidentalis* and *P. erythrorhynchos,* J. Jones, unpub. data). Examples from land birds include the cooperative hunting behavior exhibited by Harris' Hawks (*Parabuteo unicinctus*; Mader 1979, Bednarz 1988), Golden Eagles (*Aquila chrysaetos*; Collopy 1983) and Crested Caracaras (*Caracara plancus*; Morrison 1996). Most of these instances of cooperative hunting involve highly mobile prey items; cooperative foraging for less mobile organisms is uncommon (Sullivan 1984). In this report, I detail observations of cooperative foraging behavior in the Mountain Caracara (*Phalcoboenus megalopterus*). This species is adept at ground foraging and in non-urban areas feeds on large arthropods, rodents, and birds (Brown and Amadon 1968). Breeding usually occurs between October and December with two, rarely three, eggs laid (Brown and Amadon 1968).

STUDY AREA

The observations were made in the Peruvian puna zone on the road between the towns of Quillabamba and Ollantaytambo, Department of Cuzco (13° 9′ S, 72° 14′ W; 3750 m elevation). This region is characterized by dry grasslands, dominated by genera such as *Calamagrostis* and *Festuca* with interspersed shrubs of the genera *Astragalus, Berberis,* and *Lupinus* (Parker et al. 1982). Mountain Caracaras are common in this region (Parker et al. 1982) and are often found near towns where they feed on refuse and carrion (White and Boyce 1987).

RESULTS

I observed cooperative rock-turning on four occasions from 1–6 September 1995, as I watched three individuals (two adults and one immature) foraging together on the puna grassland. The immature bird was easily distinguished by its plumage. On each occasion, one of the adults approached a large rock, walked around it, uttered a high-pitched *kieeer,* and then stood by the rock. Apparently responding to the vocalization, the other individuals joined the first at the rock and proceeded to work together to flip the rock from its resting place, with each bird using one of its talons. The bird that made the call participated in the the turning but also appeared to act as a "watcher" and was the individual responsible for prey capture. On one occasion, the item was captured by an adult which then gave it to the immature bird. No begging vocalizations were uttered by the younger bird nor did it adopt any unusual posture. Each lifting event took approximately 30 min from call

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to prey capture. This species, although a ground-foraging specialist, has weak legs (Brown and Amadon 1968). After examining the rocks (approximate dimensons 30 × 20 × 10 cm), I do not believe that one individual could have turned over any of the rocks by itself.

At no time during the days of observation was the immature bird more than 100 m from one or the other of the adults, although the adults were often separated by distances up to 500 m. In a series of 12 one-hour watches (n = 4 for each individual), I determined that the two adults appeared to spend more time foraging than did the immature bird (adult = 68.6%, imm. = 52.3%) although the difference was not statistically significant (χ^2 = 3.334, df = 1, P = 0.067).

Subsequent investigation revealed that worms or arthropods could be found under most (19 of 24) of the rocks in the vicinity; several of the rocks (5 of 24) also hid rodent runways. Examination of the surrounding grassland showed that prey items of a similar size but different taxa (e.g., grasshoppers rather than millipedes) were available without rock lifting.

DISCUSSION

Unlike most land bird species, Mountain Caracaras were not using cooperative foraging behavior to pursue and subdue large, highly mobile prey items. Rather, they required cooperation to obtain access to otherwise inaccessible prey items. While the turning over of small rocks was one of the main foraging behaviours exhibited by these individuals, the cooperative rock-turning events did not occur within the set watches and did not seem to represent a major foraging strategy for these individuals. The main difference between the cooperative behavior observed in Mountain Caracaras and that observed in other cooperatively foraging birds is that only one individual obtained food from a given foraging event; Harris' Hawks, for example, share large prey that are cooperatively caught (Bednarz 1988). This disparity in obtaining a food reward may even out over time (e.g., one of the four prey items was given to the immature bird) but there apparently is often no immediate reward for some of the individuals participating. That individuals are willing to help without a reward is perhaps indicative of the length of time these birds remain together as a foraging unit; that is, an individual is willing to help today because its turn will come eventually (see Trivers 1971 for discussion of reciprocal altruism).

Congeners of the Mountain Caracara hatch their eggs in December and fledglings are usually independent by March (Brown and Amadon 1968). As my observations took place in September, the immature member of the trio was probably a chick from a previous breeding effort and its presence, therefore, may represent delayed dispersal. Delayed dispersal is fairly common in Neotropical raptors (Mader 1981). How common delayed dispersal is in Mountain Caracaras and how it may affect the incidence of cooperative foraging, is uncertain.

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Predation by Rufous Motmot on Black-and-Green Poison Dart Frog

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ABSTRACT.—I observed a Rufous Motmot (*Baryphthengus martii*) feeding a black-and-green poison dart frog (*Dendrobates auratus*) to another motmot in the Caribbean Slope lowland rainforest of northeastern Costa Rica. Neither individual appeared to suffer any ill effects from what was probably courtship feeding. Small vertebrates are typical prey for the larger species of motmots. Blue-crowned Motmots (*Momotus momota*) have been observed consuming several species of poison dart frogs raised in captivity but captive reared frogs either do not contain, or have reduced levels of, the toxins that native frogs produce. Relatively little is known about the effects of poison dart frog toxins on predators. Presumably, the digestive system of the Rufous Motmot is capable of neutralizing the potentially toxic effects of such prey. *Received 15 Sept. 1998, accepted 15 Feb. 1998.*

Poison dart frogs have long been known to possess toxic skin secretions, and, because of their bright coloration, are thought to be aposematic to visually hunting predators such as Rufous Motmots (*Baryphthengus martii*) which presumably have excellent color vision (Brodie and Tumbarello 1977). Smith (1975) demonstrated that hand-reared Torquoise-browed Motmots (*Eumomota superciliosa*) showed an innate avoidance of snake-shaped models with patterns simulating those of coral snakes. All other snake models were readily attacked implying that aposematic coloration is a deterrent to this species. Observations indicate that Blue-crowned Motmots (*Momotus momota*) at the National Aquarium consume several species of poison dart frogs including the black-and-green poison dart frog (*Dendrobates auratus*) and phantasmal poison dart frog (*Dendrobates tricolor*). However, these frogs were raised in captivity and either do not produce or have relatively low levels of the characteristic skin toxins (Kricher 1997; C. Rowsom, pers. comm.).

At approximately 9:30 CST on 26 March 1995, an adult Rufous Motmot was observed in secondary lowland tropical forest from a hiking trail located at Estacion Biologica La Suerte, near Cariari, Limon Province, northeastern Costa Rica (10° 26′ N, 83° 46′ W). The bird landed 25 m from the trail on an exposed perch 3 m above the ground and was easily observed for approximately 4 min. After 4 min another individual landed on the same branch next to the first individual. The newly arrived motmot was carrying a black-and-green poison dart frog in its beak which it fed immediately to the first individual. It is not possible to distinguish between sexes in Rufous Motmots; however, this behavior was interpreted as a male who was feeding the female as a courtship gesture. Both individuals had diagnostic black breast marks and raquet-tails indicative of adult birds, suggesting that this was probably not a fledgling being fed. The pair continued sitting on the branch for approximately 30 min after which they flew off together into the forest. Neither individual appeared to suffer any ill effects from either grasping or consuming the poison dart frog.

The typical diet of motmots varies somewhat in conjunction with body size. Smaller species prefer insects while larger species consume insects along with other invertebrates, small ver-

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tebrates, and fruit (Orejuela 1980, Remsen et al. 1993). The Rufous Motmot consumes arthropods, other invertebrates including crabs, small vertebrates including fish, lizards and birds, as well as fruit (Remsen et al. 1993). Frogs have been reported as a dietary component of the Rufous, Broad-billed (*Electron platyrhynchum*) and Torquoise-browed motmots (Remsen et al. 1993), and Blue-crowned Motmots in captivity (C. Rowsom, pers. comm.).

The effect of poison dart frog toxins on various potential predators has received relatively little attention. Brodie and Tumbarello (1977) tested the response of garter snakes (*Thamnophis sirtalis*) to *D. auratus* offered as prey. Snakes readily mouthed, or in some cases consumed the frogs but all exhibited head shaking, mouth opening, convulsions, and loss of equilibrium. Only one snake actually died and that was after consuming its third frog. These snakes do not possess color vision and might not be influenced by the aposematic coloration to the extent that an organism with color vision would be (Brodie and Tumbarello 1977).

While motmots in general may be warned by aposematic coloration, the Rufous Motmot at least is capable of handling and consuming this particular species of poison dart frog. *Dendrobates auratus* reaches densities of 1 individual/180 m^2 in one locality at La Suerte known to be frequented by Rufous Motmots (B. Graves, pers. comm.) One pair was observed on the ground rummaging through leaf litter where they would undoubtedly encounter *D. auratus* (B. Graves, pers. comm.). The level of toxins in the frogs of this area, how the motmots physiologically handle the toxins, and the frequency with which they consume *D. auratus* remain unknown.

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Evidence Of Egg Ejection In Mountain Bluebirds

Percy N. Hébert[1]

ABSTRACT.—When the last two eggs of Mountain Bluebird (*Sialia currucoides*) clutches were replaced with another bluebird egg and one House Sparrow (*Passer domesticus*) egg, 20% (3/15) of the sparrow eggs were removed within 24 hr. None of the surrogate bluebird eggs was removed. This is the first recorded instance of interspecific egg ejection in a bluebird species, and hole-nesters in general. *Received 2 Nov. 1998, accepted 18 Feb. 1999.*

Of the approximately 140 biological hosts of the Brown-headed Cowbird (*Molothrus ater*), fewer than 7% have been classified as rejectors (Friedmann and Kiff 1985, Ortega 1998). Rejectors typically remove cowbird eggs from the nest within 24 hr of introduction (Rothstein 1982). Ejection is accomplished either by grasping the cowbird egg between the mandibles or by puncturing the egg with the beak and then lifting the egg out of the nest (Sealy 1996). Acceptors, by contrast, do not remove cowbird eggs and in most cases provision the cowbird nestling(s) (see Petit 1991, Sealy 1996).

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Unlike the Shiny Cowbird (*M. bonariensis*), the Brown-headed Cowbird infrequently parasitizes hole-nesters (Ortega 1998; but see Petit 1991). Bluebirds (*Sialia* spp.) are parasitized infrequently by Brown-headed Cowbirds (Friedmann and Kiff 1985). Cowbird eggs have been found in 0.2–2.6% of Eastern Bluebird (*S. sialia*) nests, but there are only 4 records of parasitism on Mountain Bluebirds (*S. currucoides*) and none for the Western Bluebird (*S. mexicanus*; Friedmann and Kiff 1985). These low frequencies of parasitism may be due to aggression by adult bluebirds towards female cowbirds (Gowaty and Wagner 1988). Furthermore, the cowbird parasitizes smaller hosts than itself (Friedmann et al. 1977), thus female cowbirds may be too large to squeeze through bluebird cavity entrances (Friedmann et al. 1977, Pribil and Picman 1997).

Given such low frequencies of parasitism by Brown-headed Cowbirds on hole-nesters in general (Friedmann and Kiff 1985), apparently there has been little selection pressure favoring the evolution of rejection behavior (Davies and Brooke 1989). In fact, there is only one published record of interspecific egg ejection in hole nesting species (Moksnes et al. 1990). Here I present data that indicate that Mountain Bluebirds apparently cannot distinguish between conspecific eggs, whereas they can recognize interspecific eggs as different from their own, and that these eggs are sometimes removed from the nest.

METHODS

I collected the data between May and July, in 1995 and 1996, on a population of Mountain Bluebirds nesting in boxes near Virden, Manitoba (49° 51′ N, 100° 55′ W). Nest-boxes were visited every 2–3 days during nest-building and daily during laying. Eggs were measured and weighed within 24 hr of laying, and numbered on the blunt end using a non-toxic felt marker. Once the clutch was complete, the penultimate and ultimate eggs were removed for 24 and 48 hr, respectively. To minimize the risk of abandonment, some of these clutches received one bluebird egg from failed clutches and one House Sparrow (*Passer domesticus*) egg. The presence or absence of these replacement eggs was then recorded 24 and 48 hours later when the original eggs were returned to their clutches.

Because House Sparrow eggs are very similar to Brown-headed Cowbird eggs (see Lowther 1993, Lowther and Cink 1992), I expected bluebirds to respond to a sparrow egg the same way they would respond to a cowbird egg (see also Rothstein 1977).

RESULTS

Fifteen nests received a bluebird egg and a sparrow egg, and none of these nests was abandoned. None of the replacement bluebird eggs was removed from the nest within 48 hr. By contrast, 3/15 (20%) of the sparrow eggs were removed from the nest, all within 24 hr of introduction. In 2 of the 3 ejections, the sparrow egg was removed from the nest-box, whereas in the third instance the undamaged egg ended up on the rim of the nest. For both years combined, 12 bluebird eggs were known to have been cracked or dented during measuring. Of these, one was found on the rim of the nest cup the following day, 7 were gone the following day, and 4 remained in the nest.

DISCUSSION

The results of this study indicate that Mountain Bluebirds are capable of egg ejection. Mountain Bluebirds possess several traits that Rothstein (1975) identified as pre-adaptations for the evolution of ejection behavior. For instance, Rothstein (1975) suggested that the evolution of ejection behavior would be facilitated if the hosts' eggs differed from those of the cowbird in at least two respects: base color, maculation, and size. Mountain Bluebird eggs differ from sparrow and cowbird eggs in color and maculation (see Lowther 1993, Lowther and Cink 1992, Power and Lombardo 1996). Mountain Bluebirds can remove their damaged eggs from the nest; their eggs are similar in size to those of the cowbird. Thus it can be assumed that bluebirds would be capable of removing cowbird eggs from their nests.

Given that Mountain Bluebirds are sympatric with Brown-headed Cowbirds (see Lowther 1993, Power and Lombardo 1996), and that their eggs are sufficiently different to facilitate recognition and ejection of a cowbird egg, a rejection rate of only 20% would appear to be low. However, the low rate of ejection I observed is likely an underestimate of the frequency of ejection behavior in Mountain Bluebirds. For example, Rothstein (1982) observed that American Robins (*Turdus migratorius*) are less likely to eject cowbird eggs that are introduced into the nest after laying. As I introduced sparrow eggs at clutch completion, it is thus possible that bluebirds were

less likely to eject them. Furthermore, the ejected sparrow eggs were removed within 24 hr of placement in bluebird nests. Such a quick response is typical of most rejector species (Sealy 1996) and suggests at least a moderate level of intolerance (sensu Rothstein 1982) to cowbird parasitism in Mountain Bluebirds.

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Foraging Ovenbird Follows Armadillo

Douglas J. Levey[1]

ABSTRACT.—I report an observation of a foraging Ovenbird (*Seiurus aurocapillus*) following a nine-banded armadillo (*Dasypus novemcinctus*), near Gainesville, Florida. Close attendance only while the armadillo was moving and disturbing leaf litter suggests the Ovenbird was taking advantage of increased prey availability caused by the armadillo's flushing of insects. *Received 27 May 1998, accepted 1 Oct. 1998.*

Many species of birds forage in association with groups of other species. The two most common explanations of such interspecific groups relate to decreased risk of predation and increased foraging efficiency (Bertram 1978). Foraging efficiency can be increased via several mechanisms (Morse 1970). Perhaps the least-well studied mechanism occurs when one species follows another species and captures prey incidentally flushed by the second species. Such a relationship between "followers" and "beaters" has been reported for groups of birds and groups of cattle (Scot 1984), dolphins (Evans 1987), primates (Terborgh 1983, Boinski and Scott 1988), wolves (Silveira et al. 1997), ants (Willis and Oniki 1978), and other birds (Bennetts and Dreitz 1997). Here I report an observation of an Ovenbird (*Seiurus aurocapillus*) following a nine-banded armadillo (*Dasypus novemcinctus*).

On 6 March 1998 at 10:35 EST along the rim of Paynes Prairie (Alachua County, Florida), I flushed an Ovenbird from the ground. After perching for 1–2 min, it flew to the ground within 3 m of an armadillo. As the armadillo started to move forward, the Ovenbird flew directly to it, landing approximately 30 cm from its tail and maintaining that distance of separation as the armadillo walked. I followed them for 17 min at a distance of 10–12 m. The armadillo often stopped briefly (< 10 s) to dig or push its snout into the leaf litter. The Ovenbird did not approach the armadillo's head during these times but rather remained by its tail. On two occasions the armadillo stopped for 1–2 min and the Ovenbird walked 2–3 m away from it. When the armadillo started to move again, the Ovenbird immediately resumed following it, once returning by flight. It frequently pecked at the leaf litter. I was unable to determine if these presumed foraging attempts were successful. They did not appear more frequent when the Ovenbird was following close behind the armadillo than when it temporarily foraged by itself. I did not notice any insects being flushed by the armadillo, but there was heavy shade and I lacked binoculars. I stopped my observation when the armadillo walked into a clearing and the Ovenbird did not follow.

The behavior of the Ovenbird suggests its association with the armadillo was not due to both animals being attracted to an area of high prey abundance. In particular, its close proximity to the armadillo only when the armadillo was moving suggests it was using the armadillo as a beater. A similar pattern of attendance has been noted for Double-toothed Kites (*Harpagus diodontus*), Gray-headed Tanagers (*Eucometis penicillata*), and Tawny-winged Woodcreepers (*Dendrocincla anabatina*) following Squirrel Monkey (*Saimiri oerstedi*) troops; attendance frequencies of these species were higher when the Squirrel Monkey troops were moving and foraging than when they were immobile (Boinski and Scott 1988).

Despite high levels of disturbance created by armadillos while foraging, I am unaware of any other published accounts of birds following them. Further observations are required before it can be concluded that the bird I watched was not idiosyncratic and that Ovenbirds benefit from following armadillos.

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Ornithological Literature

Edited by William E. Davis, Jr.

THE GREAT BLUE HERON: A NATURAL HISTORY AND ECOLOGY OF A SEASHORE SENTINEL. By Robert W. Butler. UBC Press, Vancouver, British Columbia. 1997: 167 pp., 30 black-and-white photos, 24 color plates, 17 numbered text figs., 18 tables. $39.95 (Canadian) (cloth).—This is a very nice book about a very interesting bird—the Great Blue Heron (*Ardea herodias*)—with a particular emphasis on the subspecies that frequents the northwest coast of North America, *A. h. fannini*. However, frequent reference to herons elsewhere broadens the scope and perspective of the book. It is more than just the study of a heron, however, it is the story of the ecology and conservation of a region. Robert Butler is certainly well qualified to tell this story—24 of the more than 150 references cited bear his name as an author. In the brief introductory chapter Butler outlines the aims of the book that include detailing the natural history of the Great Blue Heron, "a worthy symbol of the conservation of coastal habitats," along the 27,000 kms of fragmented British Columbia coastline. Chapters that follow consider in detail the habitat of the heron (the shores of temperate rainforest), the heron's food web, the sites where the heron has been studied year around, all with an historical perspective on interactions with man woven through the narrative. There are chapters on foraging, food and diet, social and territorial behavior, colonial nesting, habitat selection, population dynamics, and finally a chapter on the conservation of Great Blue Herons and the Strait of Georgia ecosystem. An epilogue concludes with the optimistic thought that many people are beginning to recognize that the environment provides more than just resources, and that restoring environments will yield great future dividends. Appendices report records of Great Blue Heron colonies, length-mass regression equations for fish, effects of increased disturbance on heron populations, and lists of scientific names of plants and animals.

The book is very well written. It is clear that the author thoroughly enjoys his research on herons (including night-vision telescopic sleuthing), and his descriptions have an almost poetic touch: "I look back on the long hours spent watching herons catch fish as an enjoyable period of my life. Perched in the shade on a prominent location overlooking spectacular scenery, the smell of the sea and arbutus leaves carried on a warm breeze, gulls and shorebirds busily feeding along the mudflat—it was hard to beat," or "On calm nights I often slept on the beach beneath the stars. I welcomed the silence of the night after a day in the colony, though the quiet was periodically disturbed by landing calls ringing from the forest." Even his descriptions of natural history phenomena make for pleasant reading: "The delicate choreographed displays of a threatening heron are exquisite."

I thoroughly enjoyed reading this book. It contained a great deal of interesting and important scientific information about Great Blue Herons, and a well articulated conservation perspective. I recommend it to anyone interested in avian biology or conservation.—WILLIAM E. DAVIS, JR.

A GUIDE TO THE IDENTIFICATION AND NATURAL HISTORY OF THE SPARROWS OF THE UNITED STATES. By James D. Rising. Illustrated by David D. Beadle. Academic Press, New York. 1996: 365 pp., 27 color plates with captions, 53 color range maps, $42.00 (cloth).—Until the last three years, those of us fascinated by details of the natural history of sparrows in North America had only Bent's life histories for a reference. With the publication of *Sparrows and Buntings—A Guide to the Sparrows and Buntings of North American and the World* in 1995, and now this guide, we have substantially more information of a recent vintage at our finger tips. This is a good book. Because of its less ambitious geographic coverage,

there is more information and greater detail for each species in this book.

Sixty-two species, from Olive Sparrow (*Embernagra rufivirgata*) through McKay's Bunting (*Plectrophenax hyperboreus*) are treated. Each species account includes information about identification, similar species, details of plumage color, voice, habits, habitat, breeding behavior, range, history, geographic variation, measurements, and technical references (for further reading). A clearly drawn, easily interpreted, color range map shows breeding, winter, and "all year" ranges for each species. Including state and provincial boundaries on the range maps facilitates their interpretation substantially. Where sufficient data exist, an additional color map, showing relative abundance, based on Breeding Bird Survey information, also is included as part of the species account. Though somewhat useful, the shading of the relative abundance maps is such that it is difficult to distinguish the shades chosen for the two middle classes of the four relative abundance categories mapped. In addition, the two middle categories of 5–20 and 20–50 individuals appear to overlap. One wonders how the computer mapping software dealt with abundances of 20 individuals and how one really should interpret the relative abundance maps.

The book is comprehensive in its coverage. Among the 62 "species" descriptions in the book are a few forms not yet elevated to full species status by the AOU Committee on Classification and Nomenclature in its 1998 check-list. These include Bell's Sparrow [considered a "group" of Sage Sparrow (*Amphispizabelli*) by AOU] and Red, Sooty, and Slate-colored Fox sparrows [considered "groups" of Fox Sparrow (*Passerella iliaca*) by AOU]. There also is substantial treatment of a number of "Alaskan rarities," including Pine (*Emberiza leucocephalus*), Little (*E. pusilla*), Rustic (*E. rustica*), Yellow-breasted (*E. aureola*), Gray (*E. variablis*), Pallas's (*E. pallasi*), and Reed buntings (*E. schoeniclus*). Two other rare North American species, Yellow-faced (*Tiaris olivacea*) and Black-faced (*T. bicolor*) grassquits, reported occasionally from the southern U.S., also are described. I also appreciated the concise comments and descriptions of subspecies for Savannah Sparrow (*Passerculus sandwichensis*), Song Sparrow (*Melospiza melodia*), and Dark-eyed Junco (*Junco hyemalis*), including tables of measurements illustrating geographic variation in size. Special introductory sections for most of the genera described in the book provide helpful additional information about intergeneric relationships among the sparrows and identify areas where more research is needed to clarify relationships among species and genera.

The illustrations by David Beadle add significantly to the book's appeal. In addition to excellent color plates, each species account is illustrated by a black-and-white drawing of the species. The artist has done an excellent job of capturing the subtle beauty of plumage colors for this generally somber-colored assemblage of species.

In general this is a good, solid, user-friendly reference book for a challenging group of North American species. It is small enough to be carried in the field, though not necessarily a "field guide" in the traditional sense. I recommend it to anyone as an exceptionally well illustrated, very readable introduction to North American sparrows.—CHARLES R. SMITH.

NATURAL HISTORY OF THE WATERFOWL. By Frank S. Todd. Ibis Publishing Co., Vista, California. 1996: 490 pp., more than 750 color photographs with captions, 164 range maps, appendix. $80.00 (cloth).—This visually stunning and informative book effectively portrays the diversity of behavior, ecology, and plumage of the more than 160 species of waterfowl. Its large format (10½″ by 13″) allows the author to display to best advantage the many fine photos that he has taken in pursuit of waterfowl and other birds, although even the heaviest binoculars will seem like featherweights after lifting this hefty tome! The book begins with introductions to natural history (Chapter 1) and taxonomy (Chapter 2), then proceeds to cover primarily typical waterfowl groups in the next 15 chapters (including chapters on "Waterfowl Oddities" and "Whitewater Ducks"). The chapter on waterfowl natural history includes a nice overview of this group and its adaptations, and many photos are included to illustrate typical comfort movements and postures. The photo legends throughout the book add infor-

mation that is sometimes not present in the text, including general information on birds. The level of detail varies for examples given in this chapter, creating some redundancy with future chapters, and many of the examples are from work on geese and swans. The inclusion of the term "gang rape" (p. 41) is inappropriate and unnecessary since the preferable terminology (forced copulation) is also used in the text, and references to "hyperactive" and "hot-blooded" males in photo legends depicting forced copulation attempts are regrettable and misleading. The taxonomy chapter includes a very brief coverage of past and current thoughts on waterfowl taxonomy. The author recognizes the need for further corroboration of more recent taxonomic treatments of this group (some of which have not been supported by recent findings), and, for consistency with other sources, he uses more traditional groups for subsequent chapters with a few exceptions.

Chapters 3–17 each begin with an overview of the similarities within the group being covered, including movements on land and in the air, basic calls, feeding habits, nesting and egg-laying, flocking, mating and family behavior, and migration. Individual species accounts follow, including descriptions of extinct species and separate accounts for each race. The description of each species is accompanied by a small color range map (on which race distributions are not delineated), and usually several excellent photos of the species in the wild. Valuable information on conservation, captive propagation, and human uses/conflicts is presented in addition to more detailed information on topics outlined in the chapter overview. Incubation period, time to fledging, conditions under which dump nesting data were collected, and nesting density are presented inconsistently within the species accounts, although further details on weight, egg and clutch size, incubation period, and fledging period are presented for each species (and race if appropriate) in the Appendix. Insights from the close observation of captives complement information from extensive field experience in many species accounts. Throughout these accounts, the author has inserted personal experiences and origins of some scientific names that add extra interest for the reader. I especially found interesting the accounts of endangered species and races within various waterfowl groups.

The accounts of the northern geese (Chapter 5), swans (Chapter 6), and eiders (Chapter 14) are some of the most complete of the volume, demonstrating the author's experience with these groups and also information available from the scientific studies of The Wildfowl and Wetlands Trust in England. These chapters are full of photos, including all of the Canada Goose (*Branta canadensis*) races, and details on the Nene (Hawaiian Goose; *Branta sandvicensis*) reintroduction project and successful Barnacle Goose (*Branta leucopsis*) conservation. Nesting densities for the eiders are well-documented, as is the solving of the mystery of the location of Spectacled Eider (*Somateria fischeri*) wintering areas. Atypical waterfowl, such as the Magpie Goose (*Anseranas semipalmata*; Chapter 3); Cape Barren Goose (*Cereopsis novaehollandiae*), Freckled Duck (*Stictonetta naevosa*), Spur-winged Goose (*Plectropterus gambensis*), Comb Duck (*Sarkidiornis melanotos*), and Pink-eared Duck (*Malacorhynchus membranaceus*) (grouped as "waterfowl oddities" in Chapter 7); and screamers (Chapter 17) are covered quite extensively in accounts that highlight the unusual traits of these species and their continued puzzling taxonomy. The author groups together and covers well the white-water ducks (Blue Duck, *Hymenolaimus malacorhynchos*; Torrent Duck, *Merganetta armata*; and Salvadori's Duck, *Salvadorina waigiuensis*) in Chapter 10, describing adaptations to this demanding environment such as their sedentary lifestyle, territorial behavior, and diet of benthic invertebrates.

The sheldgeese and shelducks, sharing strong pairbonds and an aggressive disposition, are described in Chapter 8, including especially good information on the ongoing conflicts with humans when sheldgeese use crop lands. Presented in Chapter 9 is another very pugnacious group of waterfowl that includes three flightless species, the steamerducks. The chapters on the pochards (Chapter 13), seaducks (Chapter 15), and stiff-tailed ducks (Chapter 16) present many useful photos and information on feeding and diving adaptations. Also included in these chapters are fascinating accounts of the (probably) extinct Pink-headed Duck (*Rhodonessa caryophylla-*

cea), the extinct Labrador Duck (*Camptorhynchus labradorius*) and Auckland Islands Merganser (*Mergus australis*), and the only waterfowl obligate brood parasite, the extant Black-headed Duck (*Heteronetta atricapilla*). Accounts of the whistling ducks (Chapter 4), including the White-backed Duck (*Thalassornis leuconotus*), are informative but generally short because of a lack of detailed information for many species. This general lack of information available for southern hemisphere ducks is especially evident in short accounts for these species in Chapters 11 (perching ducks) and 12 (dabbling ducks). Chapter 11 covers many of the traditional perching duck group members while recognizing that the taxonomic organization of these ducks is still changing. The account of a well-studied species, the (North American) Wood Duck (*Aix sponsa*), was disappointing in its omission of available information on dump-nesting and other aspects of its natural history. In general, members of the large dabbling duck group receive more complete coverage, including more personal observations and photos by the author, although I found some aspects of the Andean Teal (*Anas flavirostris andium*) and Puna Teal (*Anas puna*) accounts at odds with my own observations.

The Epilogue presents a balanced treatment of threats to waterfowl populations and benefits greatly from the author's own experience with the continued conservation challenges that face this group. Overall, the book is written in a style that is easy to read; a glossary is included to aid the lay reader and the Index at the end of the book facilitates finding information on particular species. Scientific names are not presented in the book except for those of waterfowl species. There are few citations in the text and the bibliography includes mostly books, limiting the use of this volume as a scientific or research reference. Despite a few reoccurring grammatical problems, the writing style conveys well the thrill of viewing waterfowl and the author's enthusiasm about his experiences with this group of birds. This book is a treat to the eyes for anyone that appreciates birds, and in addition, is at the least a good overview of waterfowl natural history. Highly recommended as a visual, general reference book for anyone interested in waterfowl.—GWENDA L. BREWER.

FAIRY-WRENS AND GRASSWRENS *MALURIDAE.* By Ian Rowley and Eleanor Russell, illus. by Peter Marsack. Oxford University Press, Oxford. 1997: 274 pp., 9 color plates, numerous maps, tables and black-and-white line drawings. $75 (cloth).—This fascinating family of birds is found only in Australia and New Guinea and consists of five genera: emu-wrens (*Stipiturus*) and grasswrens (*Amytornis*) found only in Australia, tree-wrens (*Sipodotus*) and russet-wrens (*Clytomyias*) of New Guinea, and the largest genus, fairy-wrens (*Malurus*) found in both. Several species of fairy-wrens have been intensively studied using color-banded populations and biochemical analyses and the results, particularly those relating to breeding biology, are intriguing and make for fascinating reading.

This fourth volume in Oxford University Press' series on bird families of the world provides a thorough review of this interesting family of birds by authors who have done much of the primary research on several of the species considered. The monograph is divided into two parts: the first consists of eight chapters dealing with various aspects of the biology, behavior, ecology, evolution, and conservation of the Maluridae; and the second consists of accounts of the 5 genera and 25 species that constitute the family. Chapter 2 discusses two centuries of the rather confused taxonomy of the Maluridae, including more recent biochemical studies. Chapter 3 deals with the environment, biogeography, and evolution, including plate tectonics and Gondwana breakup, past and present climates and vegetation, refugia and speciation during the past two million years, changes since human settlement, and the evolution of the Maluridae including the five main lineages of fairy-wrens and the grasswrens. Chapter 4 deals with morphology, locomotion, and feeding behavior of these largely insectivorous, ground, and shrub-dwelling birds. Chapter 5 discusses vocal communication and social organization, and includes a number of sonagrams, and a thorough analysis of courtship displays. The chapter also details the remarkable findings from electrophoresis and DNA fingerprinting studies focused on reproductive biology in fairy-wrens. Although monogamous and mated for life, extra-pair copulations outside of

the territorial family group in one study, accounted for more than three-quarters of the young! Chapter 6 is devoted to co-operative breeding and an analysis of helpers at the nest (mostly surviving young from earlier years). Chapter 7 contains a generalized life history study of the Maluridae, based mostly on long-term studies of fairy-wrens, and includes sections on nests and nest building, eggs, clutch size, number of broods, reproductive success, parasitism and predation, dispersal, and survival rates. Chapter 8, on conservation, traces the clearance and fragmentation of vegetation for agriculture, forestry, and grazing, and accompanying habitat degradation, introduction of alien plants, draining of wetlands, and changes introduced into fire regimes by Europeans. The author's analysis suggests that 5 species and 5 additional subspecies are currently threatened.

In Part II, brief accounts of each genus are followed by detailed accounts of each species. These accounts begin with descriptions of adult males and females in breeding and eclipsed plumages, of immatures and moult sequences, and typically continue with history of taxonomy, weights and measurements, field characters, voice, range and status, habitat, displays, breeding behavior, and life cycle. Each account is accompanied by a range map and sonagram(s). Additional brief accounts of groupings of species within genera are present where needed, e.g., a section on the four chestnut-shouldered fairy-wren species. The eight color plates are excellent. They include, where appropriate, depictions of adult males and females, immatures, eclipsed males, and subspecies. The color of the plates is excellent, although the breast of the Blue-breasted Fairy-Wren (*Maluras pulcherrimus*) appears bluer than I remember it in the field. A color figure, grouped with the plates, contains six photographs of typical Australian habitats. A glossary helps with terms like "samphire," "spinifex," or "billabong" that might not be familiar to everyone. The bibliography includes more than 500 references.

This is a well-written, thoroughly researched, monograph. I looked through the Acknowledgments for people who I know have done work on malurids—they were all there. This is a comprehensive book, easy to read, and loaded with interesting information about a fascinating and lovely family of birds. Anyone working on Australasian birds or with interest in avian breeding biology should have this book.—WILLIAM E. DAVIS, JR.

AVIAN CONSERVATION. By John M. Marzluff and Rex Sallabanks (Eds.). Island Press, Washington, D.C. 1998: 563pp. (no price given)—*Avian Conservation* is a collection of chapters of which about one half were presented in a symposium of the American Ornithologist's Union and Raptor Research Foundation meeting in 1996. The remaining chapters were solicited by the editors to fill gaps and to provide a land manager's perspective on relevant research for avian conservation. The book is divided into 7 parts and 31 chapters. Part 1 introduces the reader to the past and present approaches taken in conservation. Part 2 reviews a variety of techniques applied in conservation research including genetics, spatial modeling, indicator species concept, and monitoring landbirds. Part 3 provides examples of approaches used to conserve endangered and sensitive species. Part 4 deals with conservation of forested landscapes and Part 5 covers non-forested and urban landscapes. Part 6 examines conservation of birds outside North America and includes the European agricultural environment, research needs and applications for Neotropical birds, and conservation in Israel, Russia, the Mariana Islands and Australia. Part 7 is a discussion on making conservation research relevant to land managers. The aims of the authors are to review current research and identify information.

Marzluff and Sallabanks should be commended for assembling concise reviews of many important topics for conservationists and applications for land managers. Anyone interested in the latest information and status of projects aimed at conserving the Northern Spotted Owl (*Strix occidentalis*), Northern Goshawk (*Accipter gentilis*), Hawaiian Goose (*Anser sandvicensis*), Red-cockaded Woodpecker (*Picoides borialis*) and others will find this book very useful. Also anyone wishing to apply techniques such as GIS modeling of populations, understanding threats to seabirds, invasions by exotics or affects of urban en-

vironments on birds should read this book. Island Press has published an attractive book in an easy-to-read format.

This book contains a wealth of information and is an excellent review of the topic although it is biased in favor of North American issues—6 of the 31 chapters were devoted to areas of the world outside the USA, 2 of those were written by Americans, and 50 of the 58 contributors were from American institutions. Consequently, the conclusions were strongly biased towards problems perceived by Americans. The topic of bird conservation is immense and the book would have been more successful if it had dealt only with birds that use the USA. A minor annoyance is the assumption by many American authors that all readers know that place names such as Pacific Northwest, Midwestern States, the Snake River, and issues such as the enactment of the Endangered Species Act are in the USA when they are writing for a world-wide audience. Once again, if the book had been focused on birds that use the USA, these terms would have been appropriate. A more important oversight is the small amount of attention devoted to existing conservation programs in the USA and abroad. For example, the North American Waterfowl Management Plan (NAWMP) is the largest and most ambitious avian conservation program undertaken in North America. It has overcome political barriers, raised billions of dollars and set aside 1000s of hectares of wetlands in Canada, the USA, and Mexico. The success of NAWMP has prompted other programs such as the Western Hemisphere Shorebird Reserve Network (WHSRN), Partners in Flight, and the Seaduck Joint Venture. There is no or very little mention of these and many other conservation programs in *Avian Conservation.* Both NAWMP and WHSRN have been in place for many years, with well established newsletters and web sites but only one paper addressed concerns about waterfowl and it focused on the Hawaiian Goose; there were no papers on shorebirds. A few chapters on the status and trends of these and other birds would have strengthened the book considerably. There was no mention of Birdlife International's *Important Bird Areas* program in Europe, the Middle East, Canada, and Mexico, and a similar program by National Audubon Society and the American Bird Conservancy in the US was also overlooked. A review of the many approaches, their successes and failures, and the research questions they require would have greatly strengthened *Avian Conservation.* These oversights suggest that a wide gap remains between the two solitudes of research and conservation management, at least in the USA. The five chapters on land management were written by Americans and for Americans. The superb reviews in *Avian Conservation* will appeal to conservationists world-wide and should be on their shelves as an up-to-date summary of field and a reference source. However, its applicability is limited largely to a North American audience.—ROBERT W. BUTLER.

RUDDY DUCKS AND OTHER STIFFTAILS: THEIR BEHAVIOR AND BIOLOGY. By Paul A. Johnsgard and Montserrat Carbonell. University of Oklahoma Press, Norman, Oklahoma. 1996: 291 pp., 16 color photos with captions, 33 numbered text figures including line drawings and range maps, 19 tables, 13 black-and-white illustrations. $49.95 (cloth).—The collaboration of these two authors brings together a wealth of experience with wild and captive stifftails, and with studies of waterfowl natural history and behavior in general. The result is a fine book on a fascinating group of ducks that includes excellent illustrations and much detailed information. Although there are few color plates (photos of both sexes of all species covered would be helpful), there are nice illustrations of each species and excellent drawings of display behavior by the first author, many of which are tracings from films or photos.

The first section of the book covers general characteristics of the stifftails, effectively introducing a number of interesting features of this group. The summary chapters that follow make especially good use of the second author's thesis work on a variety of captive stifftails at The Wildfowl and Wetlands Trust in England. Covered as the stifftail group are members of the genera *Heteronetta, Nomonyx, Oxyura,* and *Biziura.* Although the White-backed Duck (*Thassalornis leuconotus*) and Freckled Duck (*Stictonetta naevosa*) are no

longer considered to be stifftails, some comments are still included where relevant (especially display behavior). Chapter 1 begins with a detailed historical treatment of the taxonomy of the stifftails, and concludes with a synthesis of available information and a discussion of remaining questions (some of which have recently been tackled through genetic analyses). Chapter 2 presents a detailed summary of stifftail morphology and anatomy, including a discussion of the adaptations for diving that these species possess and comparisons between them. Molts and plumages are also treated in this chapter, but in a very general way, with detailed accounts appearing in species chapters when possible. I believe that it would have been helpful to include a clear summary of at least the most common molt patterns of stifftails here as an overview. Chapter 3, General Behavior and Ecology, attempts to summarize the postures and locomotion, comfort movements, time budgets, feeding behavior, habitats, dispersal, migration, and important interspecific interactions of the stifftails. Accounts of comfort movements are unusually complete due to a combination of information obtained by the authors and previous work by Frank McKinney. Time budget data and dive durations are primarily available only from captives, and diet data are presented from previous studies on wild birds. Especially rare for waterfowl are the data on dive durations and activity budgets for ducklings.

Sex ratios, pairbonds, ritualized display behavior, aggression and territoriality, and contributions of display behavior to taxonomic relationships are presented in Chapter 4 (Comparative Social and Sexual Behavior). This chapter also is based on a mixture of data from captive and wild birds. Unfortunately, some of the sample sizes from captives are small, and there is a general lack of data on number of individuals and variability, making it difficult for the reader to interpret the level of support for the authors' statements. Also, the display information focuses almost completely on male displays in this chapter. A table of male stifftail structures and displays makes for an easy comparison of behavioral similarities, and hints at some of the recent findings on the taxonomy of this group using genetic characters. Reproductive and population biology are summarized in Chapter 5, including a plea for more studies on species other than the well-known North American Ruddy Duck (*Oxyura jamaicensis*). To underscore this point, the timing of pairbonding, breeding, and nesting, and hatching success, brood behavior, renesting, and annual recruitment in this chapter are only available in any detail for the North American Ruddy Duck. Much of this information was drawn from the same three studies. Information from more species, including data from captives, is summarized for nest site characteristics, eggs and laying behavior, clutch sizes, and duckling weights, often in tables that allow comparisons to be made between the stifftails. Nest parasitism is discussed in some detail, including an indication of reproductive success relative to host nests for North American Ruddy Duck and Black-headed Duck (*Heteronetta atricapilla*), an obligate nest parasite.

The second section of the book, Chapters 6–13, presents species accounts that include vernacular names, range of species and races, measurements and plumage descriptions, identification cues, ecology, annual cycle, social and sexual behavior, nesting and parental behavior, and reproductive success and status. Range maps have been updated and improved from Johnsgard's *Ducks, Geese, and Swans of the World* (1978). In general, the species accounts present a good degree of specific data, and sample sizes are given for measurements and some other data. Plumage and soft tissue descriptions are supplemented by references to the location of photographs or illustrations in the literature, and for each species there are detailed drawings or tracings from film of courtship display postures or sequences in addition to written accounts. Although phonetic descriptions of calls are given, sonagrams would have been useful. Identification of birds in the hand and in the field is noted, and an Appendix features a dichotomous key to in-hand identification with drawings of adults and ducklings.

The section on ecology for each species includes habitat, density, foods, foraging, and a short coverage of competitors, predators, and symbionts. Data on densities, foods consumed, and predators are unavailable for many species, and the discussions of competitors are mostly speculations about diet over-

laps with various waterbirds and other stifftails. Symbionts apparently refers to parasitic egg-laying interactions, and these data would appear to have been more appropriate in the section on nest choice. Movements and migrations, molts and plumages, and the breeding cycle are discussed as parts of the annual cycle, with limited information on wild birds for the lesser-known species. Descriptions of the mating system, territoriality, courtship and pairbonding, and copulatory behavior are included under social and sexual behavior. Again, information is limited for wild birds for a number of species, and captive studies have provided the majority of the detailed descriptions of courtship displays and copulation. The use of "rape behavior" is outdated and even in the book's Glossary the reader is instructed to "See forced copulation". The nesting and parental behavior subsection includes nest choice and egg laying, and hatching and brood-related behavior. A mixture of data from wild and captive birds expands the coverage of these topics appreciably, although in general, little information on duckling behavior is known for any of the ducks. Aspects of reproductive success and status for each species were summarized in tables in the first section of the book, so in the species accounts, the focus is primarily on population estimates and conservation challenges (although coverage is a little disappointing on this topic). Brought to light here is the especially alarming predicament of the White-headed Duck (*Oxyura leucocephala*), which is threatened by overhunting, habitat destruction, and hybridization and interactions with the introduced North American Ruddy Duck. The status of most of the southern hemisphere species has been difficult to determine because of a lack of focused studies, but as human activities continue to increase pressure on wetland habitats, we cannot afford our ignorance if these species, and many others, are to survive.

The book is peppered with a number of typographical errors, but it is quite readable and a glossary is included to aid the lay reader. In general, the references throughout both sections of the book do not seem to be as up-to-date as they could have been, probably as a result of delays between preparation and publishing. Some unpublished material supplements the text, and the references section includes sources not cited in the text. This book goes a long way towards identifying where our gaps in knowledge lie and what future studies are needed on this interesting group of birds. I recommend it as a valuable and quite easy to use resource for researchers and students of waterfowl behavior and ecology or others particularly interested in the stifftails.—GWENDA L. BREWER.

THE NUTHATCHES. By Erik Matthysen, illus. by David Quinn. T & A D Poyser, London, U.K. U.S. edition published by Academic Press, San Diego, CA. 1998: xx+315 pp., one color plate, many black & white drawings, 17 black & white photos, 103 figs., 29 tables $39.95.—Books devoted to single bird families are in vogue nowadays and several series are being published. The series coming from the Poyser company of England differs from most in that the books do not attempt to be a field guide and they have no extensive color plates. Instead most of them are thorough studies of the natural history of the species involved.

The nuthatch volume is of that nature. While treating all 24 species of the genus *Sitta,* approximately 60% of the space is devoted to the Eurasian Nuthatch (*S. europaea*). The author has spent a major portion of his professional career studying this species starting with an undergraduate thesis in 1982. The species is treated in 9 chapters: Taxonomy, Morphology and Moult; Habitat and Population Density; Foraging, Food and Hoarding; The Pair and Its Territory; Breeding Biology; Finding a Territory; Dispersal and Migration; Population Dynamics; and Nuthatches in Forest Fragments. Each chapter bristles with data, often of a sort not usually found in avian life history studies. Tables and graphs abound. Besides his own data from Belgium, the author gathered data from the literature from throughout the range of the species. The result is an exemplary life history account.

The other 23 species are treated in four chapters. In so far as possible the species are treated by the same topics as above, but understandably very little is known about some aspects of the biology of some species.

The Mediterranean Nuthatches are three

Red-breasted Nuthatch (*S. canadensis*) look-alikes: Algerian (*S. ledanti*), Corsican (*S. whiteheadi*), and Krueper's (*S. krueperi*) nuthatches. All these have very limited distribution and the Algerian Nuthatch was discovered as late as 1975. The story of the discovery of this species is told in detail. The original population estimate was 12 pairs in a very restricted area but more recently the estimate is somewhere between 500 and a few thousand pairs as the result of the discovery of additional populations. All three of these species are susceptible to threats due to loss of habitat.

The two Rock Nuthatches (*S. tephronota* and *S. neumayer*) have abandoned the forest habitat of the rest of the family and are found on rocky slopes and cliffs in dry regions from Yugoslavia to Pakistan. The two overlap in Iran and eastern Turkey, and it was not realized until 1911 that they were two species.

Fourteen species are covered under the collective heading, Oriental Nuthatches. These range from the Himalayas to the Philippines, and as many as 7 species can be found together in some parts of southeastern Asia. As might be expected many of these are not well known and the treatment is less detailed than for other species. Included in this group are the 195 mm Giant Nuthatch (*S. magna*), the Blue Nuthatch (*S. azurea*), and the Beautiful Nuthatch (*S. formosa*) both of which depart from the drab coloration of most of the family, as well as two more Red-breasted look-alikes.

The final chapter discusses the 4 New World Nuthatches: White-breasted (*S. carolinensis*), Red-breasted (*S. canadensis*), Brown-headed (*S. pusilla*), and Pygmy (*S. pygmaea*). Despite the abundance of these species none of them has been studied to the extent that *S. europaea* has. The Red-breasted is the only migrating nuthatch. The "Dwarf" nuthatches, *S. pusilla* and *S. pygmaea,* are unique in the family in having small, often overlapping, territories, communal roosts, and extra male helpers at the nest.

The evolutionary history of the *S. canadensis* superspecies which consists of one species in northern North America, three species in the Mediterranean region, and two geographically separated species in China presents an interesting puzzle.

David Quinn's black-and-white sketches, many illustrating behaviors, enhance the book and the single color plate illustrates four species that will be unfamiliar to British and American readers. As of present knowledge this appears to be the definitive work on the family Sittidae.—GEORGE A. HALL.

WORKING FOR WILDLIFE: THE BEGINNING OF PRESERVATION IN CANADA. By Janet Foster, with a foreword and an afterword by Lorne Hammond. University of Toronto Press, Toronto. Second ed. 1998: 297 pp., 38 black and white photographs, 5 maps. $21.95 (paper).—In 1904, Howard Douglas, Superintendent of Canada's Rocky Mountains Park, learned that Michel Pablo wanted to sell a large herd of bison he kept in western Montana. Although as many as 20 to 30 million of the animals had once roamed the North American continent, by the end of the Nineteenth Century their numbers had been thinned to fewer than a thousand. Pablo's herd, which he estimated at around 360 individuals, represented the largest surviving aggregation of a species that seemed to be rushing headlong into oblivion. Although American conservationists hoped to keep Pablo's bison in the United States, they failed to secure the necessary funds. At Douglas's urging, the Canadian government purchased the herd and shipped it by rail to Rocky Mountains Park.

This story is one of many fascinating episodes that Janet Foster recounts in her study of the origins of Canadian wildlife conservation. According to Foster, the first significant efforts to address wildlife decline in Canada came at the end of the nineteenth century, when a handful of senior federal civil servants began using their position and influence to push a protectionist agenda. Howard Douglas and his dedicated colleagues—Robert Campbell, Director of the Forestry Branch, Department of Interior; James Harkin, Commissioner of Dominion Parks; Maxwell Graham, Chief of the Parks Branch Animal Division; and Gordon Hewitt, Division Entomologist with the Department of Agriculture—are the main protagonists in Foster's account, which begins in the mid 1880s and ends in the early 1920s.

None of this small group was a particularly prominent public figure, and only one, Harkin,

had any formal training in the biological sciences. Yet, working together with provincial officials, other interested citizens, and their counterparts in the United States, they were remarkably successful in transforming their personal commitment to wildlife into federal policy. Fighting a pervasive belief in the superabundance of nature, a national agenda that emphasized settlement and development, a public that seemed largely indifferent to the desperate plight of wildlife, and a tradition that left resource management in the hands of provincial governments, these federal officials established national parks, created wildlife preserves, rallied public support for native species, and pushed through protective legislation and regulations. Aiding this quintet of federal civil servants was a larger cast of characters who receive much less attention in this book, including the ornithologists Hoyes Lloyd, Percy Tavener, James Fleming, and others.

Foster's account of the Migratory Bird Treaty, negotiated in the years around World War I, will be of particular interest to readers of this journal. After more than a decade of lobbying, in 1913 wildlife advocates in the United States finally secured a federal law protecting migratory birds. Fearing that the new legislation might be struck down on constitutional grounds, the bill's supporters then moved to have its provisions introduced into a treaty with Great Britain. Negotiations soon bogged down, however, when officials from the Maritime Provinces balked at the idea of eliminating spring shooting. Foster demonstrates Hewitt's central role in garnering Canadian support for this landmark treaty, which remains in effect to this day.

This book is a second edition of a work first published two decades ago. The environmental historian Lorne Hammond has contributed the only significant additions: a new foreword, which briefly describes the larger context of Foster's book, and a new afterword, which reviews the literature on Canadian wildlife conservation published since the first edition. If Foster were to write her book today, undoubtedly she would pay more attention to the contributions of sportsmen, naturalists, humanitarians, and provincial wildlife officials—all of whom have received much scholarly attention since the first edition. Yet, because her book is so well written and based on solid archival research, it remains a useful starting point for anyone interested in the early history of wildlife conservation in Canada.—MARK V. BARROW, JR.

HABITATS FOR BIRDS IN EUROPE: A CONSERVATION STRATEGY FOR THE WIDER ENVIRONMENT. Compiled by Graham M. Tucker and Michael I. Evans. BirdLife Conservation Series No. 6, BirdLife International, Cambridge, U.K. 1997: 464 pp., 6 appendices. $45.00 (paper) (in North America, contact via email: BTUCKER@SIPRESS.SI.EDU).—This ambitious compilation from 8 habitat working groups marks the third and final leg of a decadal marathon sponsored by BirdLife to promote the conservation of Europe's birds (the first two culminated in Grimmet and Jones' 1989 *Important Bird Areas in Europe* and number 3 in the BirdLife series, Tucker and Heath's 1994 *Birds in Europe: their conservation status*). Thirteen workshops were held across Europe bringing experts together to prepare conservation strategies for each of the following major habitat types: marine habitats; coastal habitats; inland wetlands; tundra, mires (bogs), and moorlands; lowland Atlantic heathland; boreal and temperate forests; Mediterranean forest, shrubland, and rocky habitats; and agricultural and grassland habitats. For each habitat type, information is provided on current distribution (with maps) and trends, its history, physical and biological processes, and its dominant flora and fauna. In addition, the chief values of habitat to humans is given, and the major threats to the habitat quality and quantity of priority bird species are identified in both text and tables. The last section of each habitat chapter then lists conservation opportunities such as legislation, financial incentives, and policy initiatives, then broad conservation recommendations are given.

The rationale for priority bird rankings is explained early in the book, providing a very useful model for other large-scale bird (or other fauna) conservation efforts around the globe. In this scheme, 5 classes are established of "Species of European Conservation Concern" (or SPECs); SPEC 1 species are of

global concern (rare, endangered, or declining populations), while SPEC 4 and 5 species have favorable conservation status in Europe. Next, priority categories (from A to D) for bird species in each habitat are established using a matrix of SPEC category × habitat importance (percent of European population using that habitat). Thus, Priority A species in any particular habitat are those most vulnerable to further losses, while Priority D species are those that are more stable and widespread, with less dependence upon that particular habitat.

Next, the principles and strategies for broad conservation initiatives in Europe are outlined, spanning across international treaties and conventions, economic instruments, and policy doctrine. A dazzling litany of some 25 legislative instruments are reviewed, from global to more local European perspectives, ranging from specifics (agricultural nitrate control policy) to broad measures of biodiversity (so-called Rio Convention of 1992). Then, numerous economic instruments are reviewed (e.g., various European Union, EU, and World Bank funds) followed by other broad initiatives (e.g., Birds and Habitats Directives in EU). It would seem that with this bewildering array of conventions and plans cutting across landscapes and political boundaries, that Europe's conservation needs would all be well taken care of! But alas, as with most large Plans, "the devil is in the details"—developing consensus for habitat protection, harvest criteria, or emission standards among an array of nations with vastly different ideologies and histories in human-nature interactions is difficult.

A survey across the habitat chapters reveals the following order (from most to least) from the perspective of priority species: (1) Agricultural and grassland species—173 species (ca 70% unfavorable conservation status), with 6 Priority A species (4 are SPEC 1); (2) Boreal and temperate forests—114 species (40% unfavorable status), with 2 Priority A species; (3) Inland wetlands—102 species (55% unfavorable), with all 8 Priority A species being SPEC 1; (4) Mediterranean forest, shrubland, and rocky habitats—100 species (65% unfavorable), with 10 Priority A species (1 SPEC 1); (5) Coastal habitats—75 species (70% unfavorable), with 13 Priority A species (5 are SPEC 1); (6) Tundra, mires, and moorland—73 priority species (37% unfavorable), with only 2 Priority A species (1 SPEC 1); (7) Marine habitats—62 species (45% unfavorable), with 6 Priority A species (1 SPEC 1); (8) Lowland Atlantic heathland—16 species (all small populations), no Priority A or B species.

Some recurrent themes are the need to integrate habitat conservation planning with other sectors and programs using mechanisms such as Environmental Impact Assessment and Strategic Environmental Assessment, to modify established policies within the EU such as Common Agricultural Policy and Common Fisheries Policy to work toward sustaining biodiversity rather using the more myopic traditional focus, to remove economic incentives that destroy habitat and reduce diversity (e.g., non-indigenous tree plantations), to better educate the public about the benefits and ecological services of such natural habitats, and to work to develop standards and criteria for sustainability of habitats across national boundaries. The fact that nearly 40% of Europe's bird species show an unfavorable conservation status is largely due to *intensification*. That is, intensification of farming and silvicultural practices on land, aquaculture and open sea fishing in coastal and marine habitats, and of coastal development, recreation, and tourism, much of the latter especially in Mediterranean Europe.

This book represents an enormous effort by many experts. The details are displayed in the extensive appendices, the figures and tables are very useful in summarizing the vast amounts of species, habitat, and threat information, and the chapters are neatly and coherently packaged so that they can nearly stand alone for those with more specific interests. The approaches taken in prioritizing the species and their threats, and the conservation recommendations made by each habitat working group provide an extremely valuable reference for bird conservationists in *any* continent, not simply Europe. The challenges now lie in translating all of those directives, conventions, and biodiversity initiatives into real Action Plans that can survive the turbulent political and economic seas, especially as the new Euro currency takes hold. This book should be a library requisite for conservation-

ists, land managers, and environmental policy professionals because it transcends issues of bird conservation and prompts us to consider true integration not just of land- and ocean-scapes and their intersections, but also of ecology, agriculture, forestry, fisheries, economics, and of course, politics.—R. MICHAEL ERWIN.

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Announcement

The Lincoln Park Zoo Scott Neotropic and Africa/Asia Funds support field research in conservation biology around the world. The Scott Neotropic fund focuses on projects undertaken in Latin America and the Caribbean. The fund emphasizes the support of graduate students and other young researchers, particularly those from Latin America. Since 1986, the fund has awarded over 126 grants in 19 countries. The Africa/Asia fund, lauched in 1997, focuses on projects throughout Africa, Asia, and the Pacific. Each fund supports projects of young conservation biologists and between 5 and 15 projects for each fund are supported each year. The fund awards are seldom greater than US$7500, and most awards fall in the range of $3000–$6000. Initial support is for up to 12 months from the date of award, and the maximum duration of support is two years. The current deadline for receipt of Scott Neotropic proposals is 1 September, and Africa/Asia proposals have no deadline for 1999. For additional information and application procedures go to www.lpzoo.com, email steveed@ix.netcom.com, or write to: LINCOLN PARK ZOO SNF/AA FUNDS, % Director of Conservation and Science, Lincoln Park Zoo, Chicago, IL 60614.

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SUGGESTIONS TO AUTHORS

See Wilson Bulletin, 110:152–154, 1998 for more detailed "Instructions to Authors."

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Submit four copies of manuscripts intended for publication in *The Wilson Bulletin*, neatly typewritten, double-spaced, with at least 3 cm margins, and on one side only of good quality white paper. Do not submit xerographic copies that are made on slick, heavy paper. Tables should be typed on separate sheets, and should be narrow and deep rather than wide and shallow. Follow the AOU Check-list (Seventh Edition, 1998) insofar as scientific names of U.S., Canadian, Mexican, Central American, and West Indian birds are concerned. Abstracts should be brief but quotable. Where fewer than 5 papers are cited, the citations may be included in the text. Follow carefully the style used in this issue in listing the literature cited; otherwise, follow the "CBE Scientific Style and Format Manual" (AIBS 1994). Photographs for illustrations should have good contrast and be on glossy paper. Submit prints unmounted and provide a brief but adequate legend for each figure with all captions on a single page. Do not write heavily on the backs of photographs. Diagrams and line drawings should be in black ink and their lettering large enough to permit reduction. Original figures or photographs submitted must be smaller than 22 × 28 cm. Alterations in copy after the type has been set must be charged to the author.

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A NEW SPECIES OF HAWK-OWL *NINOX* FROM NORTH SULAWESI, INDONESIA

PAMELA C. RASMUSSEN[1]

ABSTRACT.—A distinctive new species of hawk-owl, *Ninox ios,* is described from a specimen collected in 1985 in forest at 1120 m in Bogani Nani Wartabone (then Dumoga-Bone) National Park, North Sulawesi, Indonesia. It was previously identified as a rufous morph of the Ochre-bellied Hawk-Owl, *N. ochracea. Ninox ios* is small, predominantly bright chestnut, and lacks facial patterning; it has pink orbital skin, yellow irides, triangular whitish scapular spots, a finely banded and relatively long tail, unusually short, slender tarsi that are feathered for most of their length, and weak claws. Its relationships within the genus *Ninox* are unclear; it differs in several morphological characters from all other species. Because *Ninox ios* is only known from one specimen, its distribution and conservation status are unknown; nothing is known of its ecology, but it probably occurs primarily at higher elevations than *N. ochracea. Received 14 Dec. 1998, accepted 5 May 1999.*

For many years two endemic species of the genus *Ninox* were thought to occur on the central Indonesian island of Sulawesi. Of these, the Speckled Hawk-Owl (*Ninox punctulata*) primarily inhabits disturbed lowland habitats throughout the island (White and Bruce 1986), and is morphologically quite different from other endemic Indonesian *Ninox.* The poorly known Ochre-bellied Hawk-Owl [*N. ochracea* (= *perversa*)] of the lowland rainforests in North and Central Sulawesi (White and Bruce 1986) is a small, fairly typical member of its genus (Frontispiece). Because there had been no indication that a third species might occur, it was a surprise when in 1985 F. G. Rozendaal netted an almost entirely bright rufous *Ninox* (Frontispiece) in Bogani Nani Wartabone (then Dumoga-Bone) National Park, North Sulawesi, Indonesia (Fig. 1). He concluded that this individual represented "a previously undescribed rufous phase" of *N. ochracea* (Rozendaal and Dekker 1989), and this treatment was followed by Coates and Bishop (1997).

While working on small owls at the National Museum of Natural History/Naturalis, Leiden (NNM, formerly Rijksmuseum van Natuurlijke Historie, RMNH) in June and October 1998, I chanced to see the rufous Sulawesi specimen, which had been registered as RMNH 84701 but had not yet been incorporated into the main collection following its purchase by NNM. On the second occasion I noted that it differed in several morphological features from *Ninox ochracea,* in addition to

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FRONTISPIECE. Cinnabar Hawk-Owl (*Ninox ios,* upper two) compared with Ochre-bellied Hawk-Owl (*N. ochracea,* lower left), and Buru race of Moluccan Hawk-Owl (*N. squamipila hantu,* lower right). Original watercolor painting by Ian Lewington.

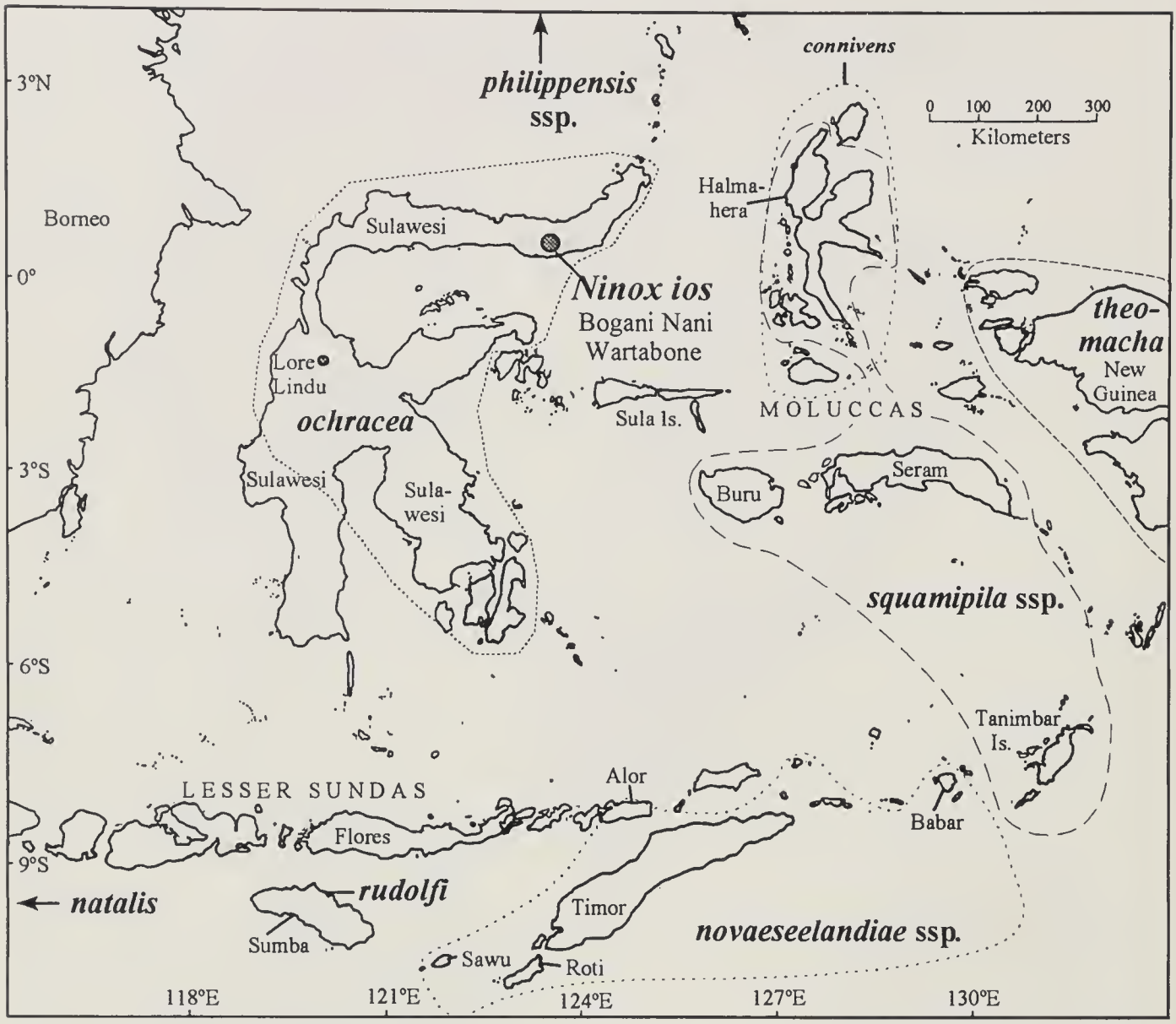

FIG. 1. Map of Wallacea showing collection locality of the holotype of the Cinnabar Hawk-Owl (*Ninox ios*), other locations mentioned in the text, and approximate ranges within the region of other species of *Ninox* and subspecies of *W. scutulata*, which occurs throughout the region.

the obvious color differences. Subsequent mensural analyses of series of all species of *Ninox* have confirmed the distinctness of the rufous Sulawesi specimen (an adult in good condition) in many characters. Although several *Ninox* species from other areas are typically rufous, morphism (and thus true rufous morphs) appears to be unknown for any *Ninox,* and in any case most of the differences are structural and thus would not be related to morph. Despite the fact that only one rufous specimen is known thus far from Sulawesi, there is no reason to believe that any of its several novel character states are aberrant, and there can be no reasonable doubt that it represents a new species.

CINNABAR HAWK-OWL *Ninox ios* sp. nov.

Holotype.—RMNH 84701, adult male (Frontispiece), according to the label collected in a forested valley at 1120 m at Clark's camp (Hill 1440), east-central Bogani Nani Wartabone National Park, North Sulawesi, Indonesia (ca 0° 40′ N, 123° 0′ E) by F. G. and C. M. Rozendaal the night of 5–6 April 1985 (the label date of 7 April presumably indicates date of death). Label data: "Completely ossified skull", "weight 78 g".

Diagnosis.—A small, lightly built, nearly uniformly rich chestnut hawk-owl with a relatively long tail and narrow pointed wings, lax feathering, no facial pattern, mostly feathered

short slender tarsi, and rufous, narrowly dark-barred wings and tail.

Compared with all flying states of *Ninox ochracea* [n = 20 (three of which are fully grown juveniles); 6 males, 4 females, 10 unsexed], *N. ios* is much smaller in most dimensions (Table 1, Fig. 2), but has a relatively longer tail and rictal bristles. Its wing, while shorter than that of *N. ochracea,* is narrower and more pointed (Fig. 3). *Ninox ios* has a much shorter, shallower bill and smaller nares than *N. ochracea.* It has short, slender tarsi that are mostly feathered on both surfaces, whereas *N. ochracea* has longer, stout tarsi that are largely unfeathered on the anterior (acrotarsal) side and are virtually unfeathered on the posterior (plantar) side, with numerous stiff bristles over the unfeathered areas. The new species has relatively sparse, fine rufous bristles on the extreme lower tarsi and on its slender toes (although the bristles are heavier and longer on the hallux), while *N. ochracea* has more profuse, heavier, mostly pale bristles (which are usually longer but sometimes worn down to stubs) on the tops and sides of its stouter toes. *Ninox ios* has much smaller, more slender claws that are dark for most of their length (vs large and mostly pale in *N. ochracea*). The holotype of *N. ios* had pink orbital skin (vs blackish in *N. ochracea*) and yellow eyes, as does *N. ochracea* according to Stresemann (1940), who based this statement on G. Heinrich's specimens [although Meyer and Wiglesworth (1898) mentioned a brown-eyed *N. ochracea*]. The base of the bill and the cere of *N. ios* appear entirely pale (vs the basal two-thirds conspicuously dark in specimens of *N. ochracea*).

In plumage, *N. ios* differs conspicuously from both adults and juveniles of *N. ochracea* in its overall bright rufous coloration (vs dark brown and yellow-ocher). Unlike all flying stages of *N. ochracea,* it lacks facial patterning, including the whitish supercilia typical of most of its relatives, and also lacks white markings in the wing coverts and flight feathers. Less obvious distinctions from *N. ochracea* include its more triangular (vs squarer tipped) whitish scapular spots, its mainly rufescent rictal bristles (vs blackish with white bases), its more narrowly barred rectrices, its vaguely dark-scalloped lower underparts (vs plain ocher or somewhat brown-streaked), and the patterning of its breast feathers, which have a light rufous (vs dark brown) area surrounding the whitish shafts.

The Philippine Hawk-Owl (*Ninox philippensis*) superspecies (sensu Dickinson et al. 1991, but see Collar and Rasmussen 1998) is composed of several dark brown to brown-and-ocher forms that are either barred or streaked below. None of the taxa included in *N. philippensis* can be described as warmer-toned than rufescent brown. All have much heavier claws and relatively shorter tails (Fig. 2A) than *N. ios,* from which they also differ in wing shape (Fig. 3). One form, *N.* [*philippensis*] *mindorensis* (see Frontispiece), is somewhat similar in overall size and tarsal feathering to *N. ios* than is any other taxon, including *N. ochracea* (Fig. 2C), but not in plumage or the above-mentioned shape characters.

All taxa of the paraphyletic Moluccan Hawk-Owl (*Ninox squamipila*; split provisionally into at least three species by Norman et al. 1998) are considerably larger and heavier-legged than *N. ios,* and all differ from it additionally in having whitish-barred underparts and scapulars. Despite the above differences, *Ninox s. hantu* (Frontispiece) of Buru superficially resembles the much smaller *N. ios* because of its overall rufescence and reduced barring below, as well as its obscure facial pattern and finely barred tail. The Sumba Hawk-Owl (*N. rudolfi*) is large and strikingly different, with a heavily spotted crown, barred underparts, and broadly banded and speckled upperparts. The widespread and variable Brown Hawk-Owl (*Ninox scutulata*) is also a much larger species, with a broadly banded tail and large, heavily feathered tarsi. It is dark brown above with the underparts heavily streaked, or nearly solid dark brown in *N. s. obscura* of the Andamans. The nominate race of the Andaman Hawk-Owl (*N. a. affinis*) is smaller than *N. scutulata,* to which it is otherwise quite similar, while the larger Nicobar race (*N. a. isolata*) is even more like some races of *N. scutulata.*

The highly varied subspecies (including a new one described from Roti Island, southwest of Timor, Lesser Sundas; Johnstone and Darnell 1997) usually grouped in the Southern Boobook (*Ninox novaeseelandiae*) as well as the Manus Hawk-Owl (*N. meeki*) are also

TABLE 1. Mean ± SD, *n* for measurements (mm) of species of *Ninox* close in size to *N. ios* (much larger taxa are not included). Ranges are given in parentheses for *Ninox ochracea*. Shortfalls of each primary were measured from the wingpoint, P1 shortfall being the distance from the outermost primary tip to the tip of the longest primary of folded wing, etc. Tarsal feathering was measured from the tip of the most distal plumaceous feather to the joint of the phalanges 1–2 of digit three.

Character	*ios*	*ochracea*	*philippensis* superspecies		
			mindorensis	*philippensis*	*spilocephalus*
Culmen length (from skull)	17.9	23.5 ± 1.5, 17 (20.6–25.7)	20.7 ± 1.0, 25	21.6 ± 1.2, 76	23.1 ± 1.1, 40
Auricular length	22.6	21.1 ± 2.7, 19 (16.5–25.7)	23.5 ± 3.5, 27	26.7 ± 3.7, 69	29.2 ± 3.9, 42
Rictal bristle length	23.9	19.6 ± 2.1, 16 (14.0–22.4)	19.9 ± 1.9, 26	21.3 ± 2.0, 68	22.3 ± 2.2, 40
Wing length	172	185.2 ± 5.8, 19 (176–195)	164.0 ± 5.2, 27	171.5 ± 6.7, 70	170.4 ± 6.3, 38
P1 shortfall	53	53.0 ± 4.0, 18 (47–60)	52.7 ± 4.1, 26	51.6 ± 3.1, 67	52.9 ± 4.7, 32
P2 shortfall	16	20.2 ± 3.8, 15 (15–29)	22.4 ± 2.1, 26	21.8 ± 4.8, 65	21.6 ± 3.5, 33
P3 shortfall	2	4.3 ± 1.9, 17 (2–9)	7.1 ± 1.7, 25	6.0 ± 1.9, 62	6.3 ± 2.6, 33
P4 shortfall	0	0.3 ± 0.8, 17 (0–3)	1.4 ± 1.2, 26	0.4 ± 0.7, 61	0.6 ± 0.9, 32
P5 shortfall	2	1.4 ± 1.4, 15 (0–4.3)	0.3 ± 0.8, 26	0.4 ± 0.9, 59	0.4 ± 0.7, 34
P6 shortfall	11	7.9 ± 2.0, 17 (5–11.4)	4.6 ± 2.1, 26	5.6 ± 2.1, 57	5.7 ± 2.1, 30
P7 shortfall	21	19.0 ± 2.6, 16 (15–22)	13.2 ± 2.6, 26	15.4 ± 2.3, 53	15.0 ± 3.0, 30
P8 shortfall	33	31.7 ± 2.6, 16 (28.9–38)	23.1 ± 2.7, 25	25.1 ± 2.8, 50	24.9 ± 2.6, 29
P9 shortfall	39	41.7 ± 2.7, 16 (38–46)	31.4 ± 2.8, 24	33.6 ± 3.2, 50	33.8 ± 2.4, 29
P10 shortfall	47	49.1 ± 2.9, 16 (43–55)	38.6 ± 3.3, 23	40.9 ± 3.8, 49	42.3 ± 2.8, 29
Tail length	97	98.3 ± 6.1, 17 (88.6–109)	82.9 ± 3.9, 27	80.9 ± 4.5, 75	76.1 ± 5.2, 36
Tarsus length	22.6	29.6 ± 1.4, 18 (26.5–32)	29.2 ± 2.3, 26	29.8 ± 2.2, 77	29.8 ± 1.6, 40
Minimum tarsus width	3.0	3.8 ± 0.3, 16 (3.4–4.6)	3.6 ± 0.2, 25	3.7 ± 0.3, 60	3.8 ± 0.3, 35
Midclaw length	9.8	11.3 ± 0.5, 16 (10.3–12.7)	11.2 ± 0.7, 26	11.6 ± 0.7, 78	11.6 ± 0.8, 40
Unfeathered tarsus	11.6	17.8 ± 3.0, 19 (13.6–24.3)	13.0 ± 1.9, 25	15.2 ± 2.3, 65	16.1 ± 2.2, 36

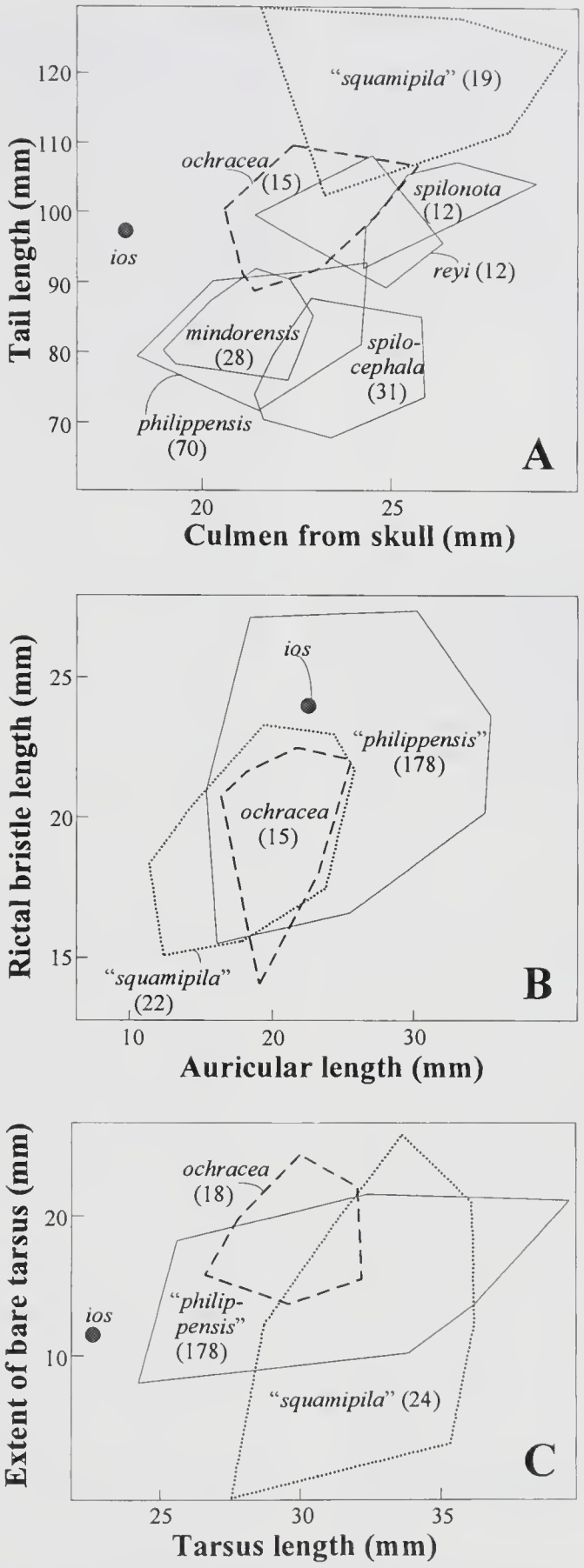

FIG. 2. Bivariate scatter plots (measurements in mm) for *Ninox ios* (filled circles), *N. ochracea*, *N. "squamipila"* (sensu White and Bruce 1986), and *N. philippensis* (sensu Dickinson et al. 1991): A. culmen vs tail length; B. auricular vs rictal bristle length; and C. tarsus length vs extent of unfeathered tarsus. For A, the main Philippine taxon groups are treated separately, while for B and C they are combined.

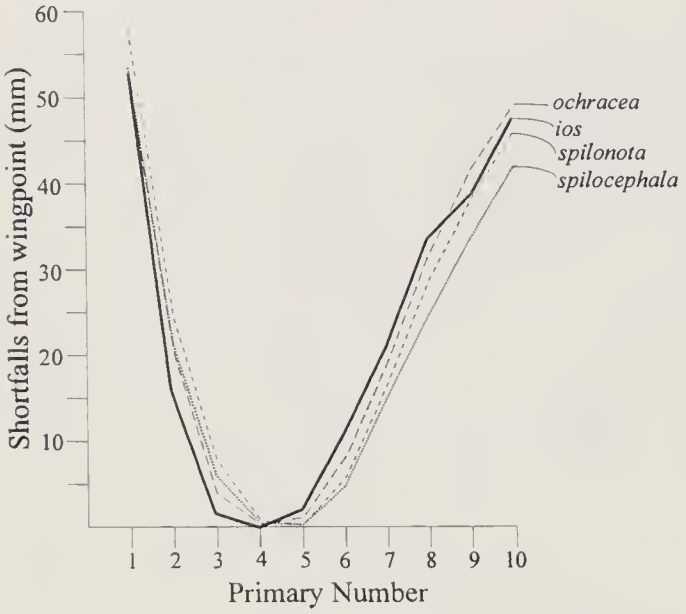

FIG. 3. Shortfalls from wingpoint of each primary (P1 = outer primary; shortfalls are distance of tip of each primary from longest primary in folded wing) for *Ninox ios, N. ochracea, N.* [*philippensis*] *spilocephala,* and *N.* [*p.*] *spilonota. Ninox p. philippensis* and similar races are virtually identical in pattern of primary shortfalls to *N.* [*p.*] *spilocephala* and thus are not shown separately, while all bar-bellied populations in the *N. philippensis* superspecies are similar to race *N. p. spilonota.*

larger than *N. ios* and are streaked or heavily blotched below. None of the remaining Australasian taxa (Papuan Boobook Owl, *N. theomacha*; Rufous Owl, *N. rufa*; Powerful Owl, *N. strenua*; or Barking Owl, *N. connivens*) approach *N. ios* more closely than the above. The other Sulawesi endemic, Speckled Hawk-Owl *(N. punctulata)*, and some Melanesian taxa (Bismarck Hawk-Owl, *N. variegata*; New Britain Hawk-Owl, *N. odiosa*; and Solomons Hawk-Owl, *N. jacquinoti*) are strikingly different in plumage and morphology, with short tails, very heavy tarsi, and *Athene*-like plumage pattern and toe bristles; in fact some had been placed in that genus (among others) in the past. The White-browed Owl (*Ninox superciliaris*) of Madagascar is very different from other *Ninox* (H. F. James, pers. comm.) as would be predicted by its distribution.

Distribution.—To date *Ninox ios* is known only from the type locality in North Sulawesi, Indonesia. It might occur at similar elevations elsewhere in the Minahasa Peninsula of North Sulawesi.

Description of the holotype.—Color matching was done under natural light using Munsell (1977) notation, in which the first number and letters refer to the hue, the number preceding the slash is the value or lightness, and the last number is the chroma or saturation. The holotype was directly compared with 11 specimens of *N. ochracea* (including the holotype) at NNM, and a series of photographs of it was compared to specimens from other museums.

Front of head from base of bill through center of forecrown and including supercilia, uniform rich chestnut (5YR 5/8); center of crown through mantle slightly darker (close to 5YR 4/6); rictal bristles fairly long (maximum 24 mm), profuse, and dark chestnut, somewhat blackish near tips; auriculars with fairly long distally extended barbs (total length of longest feather 23 mm) that are paler basally (5YR 5/10) and grade to black near the tips; chin and throat paler chestnut (5YR 6/8) than forehead.

Sides of neck and breast, back, rump, and uppertail coverts are all approximately the same rich dark chestnut (5YR 4/8). The underparts appear very lightly dappled, slightly paler chestnut (5YR 5/8) than upperparts. Most breast feathers have pale shaft streaks (5YR 7/8) and pale rufous surrounding areas, some with darker dappling at sides, and feathers of lower underparts are mostly pale rufous with vague darker scalloping (2.5YR 5/8); undertail coverts rufescent whitish with the tips scalloped rufous (5YR 6/8).

The scapulars have large mostly triangular whitish spots with broad dark chevron-shaped tips (5YR 4/4). The upper secondary coverts are almost uniformly rufous (5YR 6/8) and the upper primary coverts are darker (5YR 4/2). The remiges are faded, pale, and worn, in striking contrast to the fresh, richly colored scapulars. The inner webs of the primaries and narrow vague dark bands of the outer webs are dark grayish brown (5YR 4/4); only the outer webs have broader light bands (5YR 7/6). The base color of the secondaries is dull rufescent ochraceous (7.5YR 6/8), with fine dark dusky brown bars (7.5YR 4/4). The inner webs of the undersurfaces of the inner primaries and secondaries are basally pale rufous (7.5 YR 8/6), as are the uppersurfaces of the inner webs of the inner secondaries, which contrast strongly with the dark bands. The underwing coverts are solid pale rufous (7.5YR 7/8). The uppertail surface has pale bands of

dull rufous (5YR 5/6) that are narrow basally and wider distally, and about 12 narrow very dark brown bands (5YR 3/2) that fade out toward the tip. There are no definite bands for the terminal 20 mm. The rectrices are heavily worn and faded.

The short, slender tarsi are completely feathered with short pale cinnamon (7.5YR 7/6) pennaceous feathers to about 12 mm anteriorly (measured from joint of digits 1–2 of middle toe) and posteriorly to about 6 mm (measured from base of hallux). The toes appear to have been slender, with sparse, short rufous bristles on the tops and sides of each toe. The claws are small, delicate, and mostly blackish but with pale bases.

The soft part colors recorded on the original label are: eyes "bright yellow; pink orbital skin", bill "ivory", feet "pale whitish-yellow".

Measurements of the holotype (by author).—Culmen (from skull) 17.9 mm; culmen (from distal edge of cere) 10.7 mm; tarsus 22.6 mm; wing 172 mm; tail 97 mm. Total length of prepared specimen 220 mm. See Table 1 for measurements of other characters of the holotype and those of other species.

Etymology.—This new species is named *Ninox ios* (Greek for rust) for its striking overall coloration. The specific epithet is here used as a noun in apposition to *Ninox,* which, although usually treated as feminine, is a portmanteau combining *Nisus* and *Noctua.* The common name "cinnabar" also refers to its predominant color, which is similar to that of mercuric sulfide before prolonged exposure to light.

DISCUSSION

Voice.—Not definitely known. Rozendaal (Rozendaal and Dekker 1989:97) mentioned "disyllabic calls ascribed to [*N. ochracea*] recorded at Clark's camp and on the summit of G.[unung] Muajat during April 1985." Ekstrom and coworkers (1998:39) reported "an unknown owl *Ninox* sp." giving a series of dry hoots rising and falling in pitch in dense evergreen valley forest near the eastern boundary of Lore Lindu National Park, at about 1300 m, in the northern part of central Sulawesi (J. Tobias, pers. comm.). Either of these reports might refer to *Ninox ios* but confirming field data are required.

Habitat and elevation.—Most researchers have considered *N. ochracea* to be restricted to the lowlands below 800 m (Stresemann 1939, White and Bruce 1986, Stattersfield et al. 1998). More recently, Coates and Bishop (1997) gave the elevational range of *N. ochracea* as up to 1780 m, but this was probably based on the questionable vocal records mentioned in Rozendaal and Dekker (1989) and the collection of the type of *N. ios* at 1120 m. All montane records of *N. ochracea* therefore require review in light of this new species. *Ninox ios* clearly occurs in sympatry with, although very likely at higher elevations than, *N. ochracea.*

Molt, breeding, and ecology.—The holotype of *N. ios* clearly had recently molted its scapulars, which were bright and fresh and contrasted strikingly with the relatively dull tertials and other flight feathers. The feathers on the crown appeared to be worn, while those of the back appeared fresh. Only 10 rectrices were present. Active molt of the flight feathers was not detected, but avoid damaging the unique specimen a thorough examination was not attempted. The size of the label drawing of the largest testis (which measures 6 × 4 mm) suggests a bird not completely reproductively quiescent. Because nothing is known of the habits of *N. ios,* it is possible only to speculate that its morphology (which recalls that of owlet-nightjars Aegothelidae) suggests the likelihood of its preying largely upon soft-bodied invertebrates caught in flight.

Systematics.—The affinities of *Ninox ios* are unclear; it shows many morphological differences from all other species, particularly in its small size, relatively long tail, narrow pointed wing, and weak tarsi and claws. Although membership in the polytypic *N. philippensis* superspecies might seem geographically plausible, the pattern of primary feather lengths shown by *N. ios* is closer to that of *N. ochracea* than to any form of *N. philippensis.* Phylogenetic analyses will be required to understand the relationships of *N. ios.*

Conservation.—As only one specimen is known, it appears likely that *Ninox ios* has a limited range and/or is rare. However, nocturnal birds are frequently overlooked. Also, most scientific bird collecting in Sulawesi took place before mist-nets were widely available, and at lower elevations. Ascertaining its

vocalizations and calling periods will be a prerequisite to carrying out effective surveys, which will be essential to establish the degree of risk faced by this unique new species.

The only other bird species thought to be restricted to North Sulawesi is the poorly known Matinan Flycatcher (*Muscicapa sanfordi*), which has been found only in the Dumoga-Bone and Tentolo-Matinan mountains between 1400 and 1780 m. The fact that a species as distinctive as *Ninox ios* could have escaped description until now clearly underscores the fact that our knowledge of the avifauna of Sulawesi is still in a rudimentary state.

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PATTERNS OF VARIATION IN SIZE AND COMPOSITION OF GREATER SCAUP EGGS: ARE THEY RELATED?

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ABSTRACT.—We studied egg size variation of Greater Scaup (*Aythya marila*) nesting on the Yukon-Kuskokwim Delta, Alaska from 1991–1996. Mean egg size was 64.36 ± 0.03 (SE) ml. Egg size did not vary with clutch size or serve as an index of body size. There was less than 2% overlap in total clutch volumes for clutches of different sizes indicating that phenotypic clutch size–egg size trade-offs are not occurring among individuals. At the population level, Greater Scaup have less variation in egg size than other species of waterfowl. The proportion of variation in egg size caused by differences among females was 0.20, caused by differences within females among years was 0.25, and caused by differences within females and years (i.e., clutches) was 0.56. The proportion of egg lipid decreased with increasing egg size while the proportion of egg protein increased with egg size. Thus, Greater Scaup appear to trade-off lipid for protein as egg size increases. The proportion of variation that was due to differences among females in total egg protein was 0.79 and in total egg lipid was 0.49. We conclude that in the absence of a fitness trade-off between clutch size and egg size, selection has reduced among-individual variation in egg size. *Received 16 April 1999, accepted 4 August 1999.*

Lack (1967) suggested that trade-offs may occur between the number and size of eggs produced by waterfowl species. Rohwer (1988) argued that the same trade-off between number and size of eggs should occur within species as well. The high repeatability of egg size (i.e., volume or weight) generally found in waterfowl suggests that such trade-offs likely occur among rather than within individuals (Lessells et al. 1989, Larsson and Forslund 1992). Thus, the concept of a clutch size–egg size trade-off implies that females laying small clutches of large eggs and females laying large clutches of small eggs have equal fitness. Accordingly, for a trade-off to exist both clutch size and egg size must be positively related to fitness.

Waterfowl laying larger clutches may be more fit because they tend to fledge more young (Lessells 1986, Rockwell et al. 1987, Flint 1993). For example, Rockwell and coworkers (1987) demonstrated that female Lesser Snow Geese (*Chen caerulescens caerulescens*) laying larger clutches recruited more young than females laying smaller clutches. Fitness may also be related to egg size in some species of waterfowl because young from larger eggs are better able to survive extreme conditions (Ankney 1980, Rhymer 1988, Thomas and Brown 1988). For example, Dawson and Clark (1996) found that Lesser Scaup (*Aythya affinis*) ducklings from large eggs survived better than those from small eggs under natural conditions (but see Williams et al. 1993). The mechanism by which larger eggs yield higher juvenile survival may be related to egg composition (Dawson and Clark 1996). Egg composition, in terms of lipid and protein, typically varies isometrically with egg weight for waterfowl species (Ankney 1980, Hepp et al. 1987, Owen and West 1988, Hill 1995, Slattery and Alisauskas 1995); however, some species show a proportional increase in lipid with increasing egg size (Birkhead 1984, 1985; Alisauskas 1986; Rohwer 1986; Williams 1994). In either case, young hatching from large eggs tend to be larger at hatching and have absolutely larger reserves than young hatching from smaller eggs (Ankney 1980, Slattery and Alisauskas 1995, Erikstad et al. 1998).

Fitness trade-offs are potential mechanisms maintaining heritable variation in both egg size and composition at the population level (Falconer 1989). Egg size has been shown to be, at least partially, under genetic control, and heritable genetic variation has been found in several species of waterfowl (Batt and Prince 1978, Lessells et al. 1989, Larsson and Forslund 1992). Thus, in the absence of fitness trade-offs, mean egg size for a population

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would be expected to respond to directional selection. Therefore, we predict that patterns of egg size variation within and among populations are linked to clutch size–egg size trade-offs. Additionally, if clutch size–egg size trade-offs exist, then the corresponding variation in egg composition can be used to infer the required relationship between egg size and fitness. It follows then, that patterns of variation in egg composition within populations are also influenced by clutch size–egg size trade-offs.

Our goal in this study was to describe egg size variation in Greater Scaup (*Aythya marila*) with regard to female body size and clutch size. Further, we looked for evidence of clutch size–egg size trade-offs among females. We examined variation in egg composition within and among females and in relation to egg size and compared these results to other species.

METHODS

This study was conducted along the lower Kashunuk River drainage (61° 20′ N, 165° 35′ W) on the outer coastal fringe of the Yukon Delta National Wildlife Refuge, Alaska. This study was conducted under appropriate Federal (PRT-692350), state (93-69), and refuge special use collection permits. The study area consists of relatively flat sedge meadows and numerous ponds (Flint and Grand 1996a, Grand et al. 1997). Nest searches were conducted from mid-May through mid-July (see Flint and Grand 1996a). When nests were discovered, the number of eggs, nest location, and date were recorded. Eggs were individually numbered and candled to determine the stage of embryonic development (Flint and Grand 1996a). Nests were revisited at 7 day intervals and the number of eggs and stage of development of embryos were recorded. Maximum lengths and breadths of all eggs were measured to the nearest 0.1 mm. Clutch size was defined as the number of eggs known to have been laid into a nest for nests found during egg laying and as the number of eggs in the nest at time of discovery for nests found during incubation.

In 1994–1996 a sample of hens was captured on the nest at hatching using bow traps (Flint and Grand 1996b). Hens were weighed to the nearest 10 grams and culmen and total tarsus lengths were measured to the nearest 0.1 mm. Females were marked with aluminum U.S. Fish and Wildlife Service tarsal bands.

In 1996, we collected a sample of 30 complete clutches at 4 days of incubation in conjunction with a separate study of renesting ecology. These eggs were weighed, measured (length and breadth) with calipers, and we measured the external volume by submerging the egg and measuring the displacement of water to the nearest 0.5 ml. Variables in the relationship between volume and linear measures were estimated using analysis of covariance with volume as the dependent variable, females as a factor, and length × breadth^2 as the single covariate (Hoyt 1979, Flint and Sedinger 1992, Flint and Grand 1996b). We included the interaction between females and length × breadth^2 to compare the slope of this relationship among females. The fitted relationship was used to predict egg volume from linear measures for eggs where volume was not measured directly (i.e., eggs measured in the field).

In 1993, a sample of nests was visited every other day after 7 eggs had been laid to determine the date of clutch completion. We collected a sample of 88 eggs from 11 clutches as soon as laying was complete. These eggs were boiled for 15 min and frozen. Each egg was later thawed and weighed whole. Because entire clutches were collected at the end of laying and some incubation occurred during laying, vascularization or embryonic development was noted as being present during dissection. The egg was separated into shell, albumen, and yolk and these components were dried to a constant weight at approximately 80° C. Fat was extracted from the yolk using petroleum ether (Dobush et al. 1985) in a Soxhlet apparatus. Total yolk protein was estimated as whole yolk dry weight minus yolk fat. We assumed that dried albumen weight was composed entirely of protein (Montevecchi et al. 1983) and estimated total egg protein as total yolk protein plus albumen dry weight.

We examined variation in egg size with clutch size using a nested ANOVA with clutches nested within clutch sizes. We used the mean square error among clutches with clutch sizes as the denominator in the *F*-test of clutch size effects. Total clutch volume was calculated as the sum of the individual egg volumes within a clutch for the sample of nests that survived to incubation. We used the sum of the log transformed measurements of culmen and tarsus as an index of structural size and examined variation in mean egg size in relation to this index for the sample of nests from which we captured females using linear regression. The proportion of variation in egg size caused by differences within clutches, within females among years, and among females (i.e., repeatability) were calculated using a nested ANOVA and modifying the methods of Lessells and Boag (1987) for a nested design (Sokal and Rohlf 1981).

We examined variation in both total egg lipid and protein (separately) using ANCOVA with female (i.e., clutch) and egg development as factors and egg size as a covariate. We also included an interaction between female and egg size. To examine allometric relationships of egg components we used $\log_{10}$-$\log_{10}$ regression of egg components against egg weight; isometry was concluded if the slope of these relationships was not different from 1. Repeatability of egg components was estimated using a nested design with eggs nested within females. All analyses were conducted using SAS version 6.12 (SAS Institute 1990).

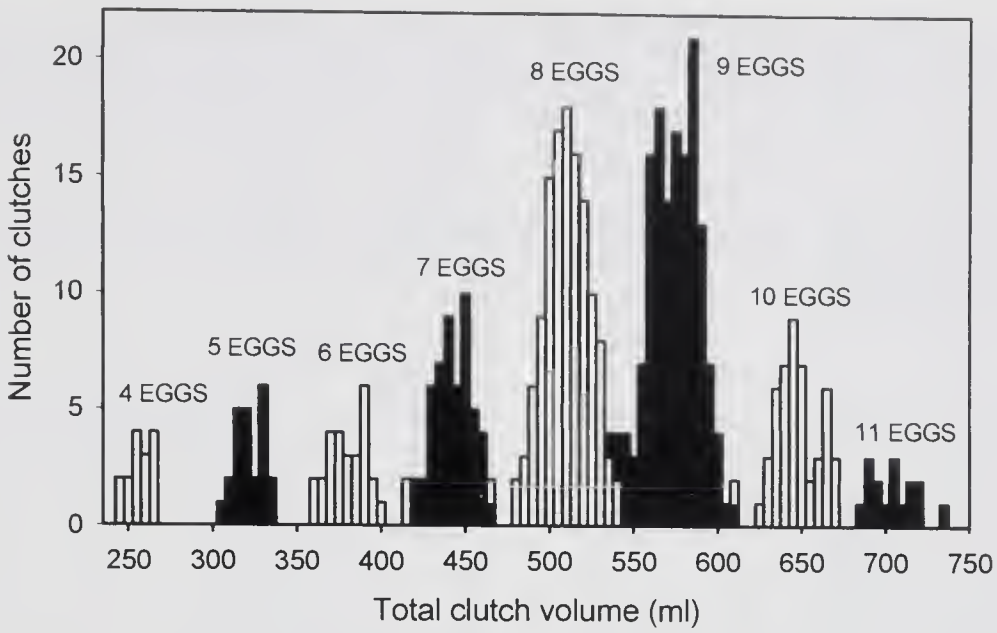

FIG. 1. Total clutch volume for Greater Scaup clutches of different sizes from the Yukon-Kuskokwim Delta 1991–1996. Clutch volumes were rounded to the nearest 5 ml. Overall only 3 of 235 (1.3%) clutch volumes (i.e., two 9 egg clutches and one 10 egg clutch) occurred within the volume distribution of another clutch size. Other stacked bars represent tied values resulting from rounding of total clutch volumes where actual estimates of total clutch volume did not overlap. For example, a 7 egg clutch with a volume of 467 ml is stacked with an 8 egg clutch of 468 ml because rounding is required to develop the distributions.

RESULTS

We measured length, breadth, weight, and volume of 271 eggs. The equation:

$$\text{Volume} = 31.84 + 0.2729 \times \text{length} \times \text{breadth}^2, \quad (1)$$

described the relationship between displacement (ml) and linear egg measurements (cm) ($r^2 = 0.44$, $F_{1,269} = 209.10$, $P < 0.001$). To compare variation in predicted egg volumes with variation in measured volumes we calculated the repeatability of measured egg volumes (33.4%) and found it similar to the repeatability of estimated egg volumes (36.4%).

We measured a total of 3937 eggs in the field. Mean egg length was 6.352 ± 0.003 (SE) cm and egg breadth was 4.328 ± 0.002 cm. Mean estimated egg size was 64.36 ± 0.03 ml (CV = 0.03). We had no data on variation in egg size with laying sequence, but the average range of egg size within clutches was 3.3 ml.

Egg size did not vary with clutch size ($F_{12,470} = 0.74$, $P > 0.05$). For the analyses of the relationship between egg size and body size we used 93 observations of individual females captured on nests. Average egg size per clutch was not related to our index of body size ($F_{1,90} = 0.35$, $P > 0.05$). Overall only 3 of 235 (1.3%) clutch volumes (i.e., two 9-egg clutches and one 10-egg clutch) occurred within the volume distribution of another clutch size (Fig. 1).

For estimates of repeatability of egg size we captured 20 females 41 times (only 1 female was captured 3 times). The proportion of variation in egg size attributed to differences among females (i.e., repeatability) was 0.20, proportion of variation attributed to differences within females among years was 0.25, and proportion of variation attributed to differences within females and years (i.e., clutches) was 0.56. Using a standard approach of calculating the mean egg size per clutch and treating clutches as individual observations within females (e.g., Flint and Grand 1996b) yields a repeatability of mean egg size of 0.36.

Total egg protein varied with egg size ($F_{1,64} = 67.96$, $P < 0.001$), but not among females ($F_{9,64} = 1.55$, $P > 0.05$). The relationship between egg protein and size also did not vary among females (i.e, no interaction, $F_{9,64} = 1.59$, $P > 0.05$). Total egg protein was not significantly influenced by early embryonic development ($F_{1,64} = 3.23$, $P > 0.05$). Similarly, total egg lipid varied with egg size ($F_{1,64} = 65.80$, $P < 0.001$), but not among females ($F_{9,64} = 1.98$, $P = 0.055$). However, the rela-

TABLE 1. Allometric relationships between total egg lipid, protein and water in relation to egg weight.

Allometric relationship	r^2	Slope	LCL[a]	UCL[a]	t^b	P
Weight and egg lipid[c]	0.62	0.85	0.71	0.99	2.09	0.04
Weight and egg protein[c]	0.84	1.11	1.01	1.21	2.16	0.03
Weight and egg water	0.95	1.01	0.96	1.06	0.52	>0.05

[a] Upper and lower 95% confidence limits for slope.
[b] Test of null hypothesis that slope = 1.0.
[c] Egg lipid and protein are in dry weight.

tionship between total egg lipid and egg size varied among females (i.e., interaction; $F_{9,64} = 2.04$, $P = 0.049$). Total egg lipid was not influenced by early embryonic development ($F_{1,64} = 0.17$, $P > 0.05$).

The proportion of lipid in an egg declined with increasing egg weight, whereas the proportion of protein increased with increasing egg weight (Table 1). Among-female differences explained most of the variation in total egg protein; whereas within-female (i.e., within clutch) differences explained most of the variation in egg lipid components (Table 2). Even with the variation in egg composition within and among females, total clutch volume still predicted most of the variation in total protein ($r^2 = 0.86$, $F_{1,8} = 48.71$, $P < 0.001$) and lipid ($r^2 = 0.93$, $F_{1,8} = 100.05$, $P < 0.001$) investment in a clutch.

DISCUSSION

Egg size.—The relationship between length × width^2 and measured volumes fit poorly ($r^2 = 0.44$) for Greater Scaup. For other species of waterfowl these relationships have shown a high r^2 (>90%; Flint and Sedinger 1992, Flint and Grand 1996b, Slattery and Alisauskas 1995). We believe this relatively poor fit is the result of the low coefficient of variation in egg size (i.e., lack of variation in the y-axis). Additionally, we likely detected variation in slope among females because we sampled entire clutches and thus had relatively large samples within females. Other studies have failed to find variation in slope of predictive relationships between egg measures and egg size among females but only sampled a few eggs from each clutch (Flint and Sedinger 1992, Flint and Grand 1996b). We found little difference between estimates of repeatability of predicted volumes and measured volumes. The comparability of these two results indicates that error associated with predicting egg volumes is random within and among females.

We found less variation in egg size at the population level than has been reported for other species of waterfowl. The coefficient of variation of average egg size for Greater Scaup (3%) was substantially less than for Northern Pintails (*Anas acuta*, 11%; Flint and Grand 1996b), Blue-winged Teal (*Anas discors*, 9%; Rohwer 1986), Canada Geese (*Branta canadensis*, 7–9%; Cooper 1978, Leblanc 1989), Black Brant (*Branta bernicla nigricans*, 8%; Flint and Sedinger 1992), or Lesser Snow Geese (8%; Cooke et al. 1995). Thus, it appears selection has reduced the variation in egg size at the population level compared to other species.

The repeatability of egg size that we measured among females is substantially lower than reported for other waterfowl (Batt and Prince 1978, Duncan 1987, Lessells et al. 1989, Flint and Sedinger 1992, Flint and Grand 1996b). When we partitioned variance using a nested ANOVA design, including variation within clutches, we found the among female component of the variance was even lower. Using an approach similar to ours,

TABLE 2. Average egg components dry weight and proportion of variation due to differences among females.

Variable	$\bar{x}$	SE	Among female variance component (%)
Albumen (g)	4.97	0.046	87.9
Shell (g)	5.23	0.032	73.2
Yolk (g)	14.84	0.109	52.4
Total egg lipid (g)	9.97	0.069	48.8
Total egg protein (g)	9.89	0.077	79.1
Lipid per ml	0.15	0.001	36.2
Protein per ml	0.15	0.001	79.9
Density (g/ml)	0.91	0.003	67.9

Leblanc (1989) reported that the proportions of variation among female Canada Geese, within females–among years, and within clutches were 0.62, 0.05, and 0.33, respectively. Thus, the patterns of egg size variation within and among female Greater Scaup are substantially different than those reported for other waterfowl. The average range of egg sizes within clutches was similar to the range of egg sizes reported for other waterfowl (Leblanc 1987, Owen and West 1988, Flint and Sedinger 1992, Robertson and Cooke 1993, Cooke et al. 1995). Thus, the low repeatability we report is not the result of relatively high variation within females (i.e., clutches), but is strongly influenced by the lack of variation in egg size among females. Relative to other waterfowl species, it appears selection has resulted in reduced egg size variation among female Greater Scaup and maintained variation within clutches that may be related to sequence (Flint and Sedinger 1992, Cooke et al. 1995).

Mean egg size did not vary with clutch size in this study. This is consistent with findings for other waterfowl (Duncan 1987, Rohwer 1988, Rohwer and Eisenhauer 1989, Flint and Sedinger 1992, Flint and Grand 1996b). Therefore, we did not detect a trade-off between clutch size and egg size predicted under the nutrient limitation hypothesis and a simple model of nutrient allocation to eggs (Flint et al. 1996). Additionally, mean egg size was not related to body size and the alternative allocation model described by Flint and coworkers (1996) cannot explain the failure to detect a negative relationship between clutch size and egg size. Finally, the lack of significant overlap in total clutch volumes for clutches of different size, indicated phenotypic trade-offs between clutch size and egg size among females with equal investments in their clutches did not occur (Flint and Sedinger 1992, Flint and Grand 1996b). Thus, we find no evidence of phenotypic clutch size–egg size trade-offs among individuals for Greater Scaup.

Ankney and Bissett (1976) proposed that egg size variation in a population was maintained by annual variation in environmental conditions that caused annual variation in optimal egg size. While not explicitly stated, the concept of a clutch size–egg size trade-off is inherent in this hypothesis. In their example, Ankney and Bissett (1976) state that the advantage to females laying small eggs is that they can produce more eggs from finite reserves than females laying large eggs. We found considerably less egg size variation at the population level than has been reported for other species. Correspondingly, we also found no evidence of a clutch size–egg size trade-off whereas studies of other species have shown some evidence of a trade-off among individuals with equal investments in their clutches (Ankney and Bissett 1976, Flint and Sedinger 1992, Flint and Grand 1996b). Further, repeatability sets the upper limit to heritability (Falconer 1989); thus, the low repeatability we measured implies little genetic variability for egg size in our study population. Traits influenced by selection are expected to approach fixation and therefore have low heritabilities (Falconer 1989). We suggest for Greater Scaup that clutch size–egg size trade-offs do not occur and selection has reduced variability in egg size.

Egg composition.—Because female waterfowl commonly begin incubation before egg laying is complete (Flint et al. 1994), and we did not collect eggs until egg laying was terminated, some eggs had slight embryonic development at the time of collection. The presence of egg development was not related to either total egg lipid or protein after controlling for variation among females, egg volume, and an interaction between females and egg volume. Thus, we do not believe that the early development observed in some of our collected eggs influenced our results.

The relationship between egg lipid and egg size for Greater Scaup varied among females. This is similar to what Rohwer (1986) found for Blue-winged Teal. Birkhead (1985) reported greater variation in egg composition among females than within clutches for Mallards (*Anas platyrhynchos*). Further, Alisauskas (1986) found that egg lipid was highly variable among female American Coots (*Fulica americana*) and varied within clutches in relation to egg sequence. Hepp and coworkers (1987) found that about half of the variation in egg lipid in Wood Ducks (*Aix sponsa*) was due to differences within females, similar to our results. Varying egg composition may allow females to slightly adjust the total investment in the clutch without altering clutch size

or egg size (Owen and West 1988). The consistent finding that egg lipid varied within females suggests that there may be some adaptive partitioning of resources within clutches, perhaps related to egg laying sequence. However, even with the variation in egg composition described above, total clutch volume explained more than 85% of the variation in total lipid and protein investment in a clutch. Thus, contrary to the results of Flint and Grand (1996b) for Northern Pintails, clutch size is a good predictor of nutrient investment in Greater Scaup clutches.

Heavier eggs had proportionally more protein and less lipid than lighter eggs. Thus, it appears that Greater Scaup trade off lipid for protein as egg weight increases. These results differ from studies of waterfowl that show a proportional increase in lipid with egg size (Birkhead 1984, 1985; Alisauskas 1986; Rohwer 1986; Williams 1994), and differ from studies of other precocial species where egg protein and lipid both increase proportionately with egg weight (Ankney 1980, Hepp et al. 1987, Owen and West 1988, Hill 1995, Slattery and Alisauskas 1995). Ankney and Bissett (1976) argued that because egg yolk, and hence egg lipid, increased with egg size, young hatching from larger eggs survived better because they had absolutely larger lipid reserves. However, young from larger eggs tend to be larger at hatch (Ankney 1980, Slattery and Alisauskas 1995, Erikstad et al. 1998) and thus will also have absolutely higher energy requirements (Rhymer 1988). For Greater Scaup, the proportion of egg lipid decreased with increasing egg size. Therefore, we would not expect large egg size to confer a survival advantage to offspring in our study population.

Given our conclusion that clutch size–egg size trade-offs do not occur, and egg size has been optimized by selection for our population, we would expect no relationship between egg size and fitness for our study population. The proportional decline in egg lipid with increasing egg size fits this prediction. Therefore, we conclude that clutch size–egg size trade-offs likely influence both egg size variation and patterns of egg composition within species. If this hypothesis is correct, we would predict that species showing evidence of phenotypic trade-offs between clutch size and egg size (e.g., Northern Pintails; Flint and Grand 1996b) would also have patterns of variation in egg composition consistent with the expectation that offspring from larger eggs have a survival advantage.

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POSTFLEDGING BEHAVIOR OF GOLDEN EAGLES

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ABSTRACT.—We predicted that extended parental care, asynchronous hatching, and incidences of siblicide in Golden Eagles (*Aquila chrysaetos*) could increase the chances for conflict between siblings, and between parents and offspring as juveniles aged. This conflict could motivate independence and dispersal in this species. To test our predictions, during the 1993 and 1994 breeding seasons we examined post-fledging behavior in Golden Eagles from the Little Missouri National Grassland and contiguous areas of western North Dakota. We collected observations of 28 radio-tagged juveniles to determine whether predispersal movements were correlated with age and with the presence of a sibling or parent during the first 6–10 weeks after fledging. We also recorded juvenile vocalization rates to determine if they changed with age or the presence of a parent. We found that distance from the natal nest increased with time since fledging. This was attributed to an increased proficiency in flight and gradual development of independence from parental care. We found that calling rate and distance between individuals of sibling pairs did not change with time after fledging but was highly variable. Calling rates of fledglings in the presence of parents were higher than when parents were absent. Increased calling may facilitate juvenile location or inform the parents of offspring nutritional status. Parents were not visible for most observation periods and we did not observe any aggression by parents directed toward offspring. Siblings engaged in "play" activity and we did not detect any signs of aggression between siblings. Our data do not support the predictions that an increase in parental and/or sibling aggression is associated with independence in this population of Golden Eagles. *Received 15 Oct. 1998, accepted 20 April 1999.*

Factors influencing the timing and duration of dispersal may be extrinsic (environmental), endogenous, or some combination of the two (Howard 1960, Ritchison et al. 1992, Belthoff and Duffy 1995). Extrinsic factors include parental aggression toward young (Alonso et al. 1987, Hiraldo et al. 1989, Wiggett and Boag 1993), sibling aggression (Holleback 1974, De Laet 1985, Strickland 1991), ectoparasitism (Brown and Brown 1992), increased predation risk (Harfenist and Ydenberg 1995), and declining food availability within the natal area (Messier 1985, Kenward et al. 1993, Bustamante 1994b). In raptors, the role of sibling and parental aggression in family break-up is disputed. In some species, dispersal may occur after a period of parent-offspring conflict, the parents being the ones who promote the independence of juveniles by gradually reducing the food supply or increasing aggression towards the juveniles (Alonso et al. 1987, Delannoy and Cruz 1988, Hiraldo et al. 1989). Family break-up may also take place without apparent conflict (Bustamante and Hiraldo 1990, Bustamante 1994b). Although Watson (1997) thought that there was little evidence of aggression between adult Golden Eagles and their young, Walker (1987) observed some aggression by parents toward offspring during the fledgling dependency period. There is little information on the factors that affect timing of dispersal in Golden Eagles because few studies have been conducted on the behavior of juvenile eagles during this stage (Watson 1997). We predicted that the extended parental care, asynchronous hatching (Watson 1997), and high incidence of siblicide (Edwards and Collopy 1983, Edwards et al. 1988) in this species would increase the probability of predispersal conflict.

METHODS

Study area.—We conducted this study from May to November 1993–1994 in the Little Missouri National Grassland (46° 00′–48° 07′ N, 102° 50′–104° 00′ W) and contiguous areas in western North Dakota. The dominant habitat was mixed prairie with patches of shrubs managed primarily for livestock grazing (Hopkins et al. 1986, Fowler et al. 1991). Woodlands (1.8% of total vegetative cover) were found in areas of higher soil moisture, such as valley bottoms, lower valley slopes, and along stream banks and floodplains of the Little Missouri River (Girard et al. 1989). Large buttes, easily eroded sandstone, and clay badlands characterized the topography. The climate is semi-arid continental with wide daily fluctuations in temperature and

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variable precipitation. Annual precipitation averages 33–41 cm, and the average temperature in July is 21° C (Jensen 1972). We found Golden Eagle nests on siltstone and clay buttes, and in trees along rivers and streams.

Data collection.—We located active Golden Eagle nests by aerial and ground surveys. We aged chicks based on behavior and plumage (Ellis 1979), and sexed them based on bill depth and head, hallux claw, and tail length (A. Harmata, pers. comm.). We entered each of the 20 eagle nests (n = 10 in 1993; n = 10 in 1994) when nestlings were 8–10 weeks of age (near fledging). We selected this age because harassment can cause prolonged absence of eagle adults which could result in nestlings being exposed to direct sunlight or missed feedings—both fatal to younger chicks. Because young eagles will fledge prematurely if disturbed, we waited until nestlings were fully feathered and could fly well enough to avoid injury if they fledged in response to our presence (Fyfe and Olendorff 1976). Twenty-eight (12 male, 16 female) chicks (n = 12 in 1993; n = 16 in 1994) were weighed, measured, fitted with a 25-g backpack-style radio transmitter (L. L. Electronics, Mahomet, Illinois), and banded with an aluminum U.S. Fish and Wildlife Service leg band. After we instrumented and measured each eagle, we placed it back in the nest where it remained until it fledged. We spent an average of 51.3 (± 3.9 SE) min from eagle capture to replacement in the nest.

We considered a juvenile as fledged after its first flight from the nest. After fledging, we located birds using ground searches every 2–4 days for behavioral observations. We recorded over 416 hr of direct behavioral observations from 14 July to 20 August 1993, and 15 July to 22 August 1994. We recorded movements of radio-telemetered birds until they dispersed from their natal territories, or we found them dead. During the first five weeks, we were usually able to locate eagles visually (94.1% of attempts). We primarily used triangulation (Kenward 1987) by four observers to find juveniles in the later stages of the post-fledging period.

We observed eagles during daylight hours (06:00–21:00 MST) using 14–45× zoom spotting scopes from vehicles or at locations at least 300 m from the bird. We determined target observation times by randomly selecting a 4-hr block of daylight. We covered the other time periods during later observations using the same method. During each observation period, we continually recorded data until the predetermined time elapsed, or until we could no longer observe the bird. We collected a mean of 15.4 (± 1.2) hr of observation per bird over 4.3 (± 0.3) observation periods. We recorded eagle locations and activities on a data checksheet. We did not record sibling behaviors simultaneously. We recorded the following data on adults: location in relation to focal bird, incidences of food deliveries by an adult, stooping and physical aggression directed toward the focal bird. We observed few prey deliveries (n = 9), so we could not analyze temporal changes in food provisioning rates.

We attempted to sample behavior equally among birds for different ages and times of day. We calculated distance from focal bird to the nest and the distance between siblings using simple geometry and UTM coordinates.

Statistical analysis.—Using Repeated Measures Analysis of Variance (ANOVA; Proc GLM; SAS Inst. Inc. 1987; PC ver. 6.10) we tested our predictions on the pooled 1993–1994 data because there were too few data to examine a year effect using repeated measures analysis. To determine the proper sampling unit for analysis (individual bird vs nest) we used the ratio of Type III Sum of Squares (Proc GLM). A relatively large ratio (>2) would indicate that individual birds should be combined into one "nest" unit because separate consideration results in unexplained error (Sum of Squared Errors; P. Chapman, pers. comm.). There was no evidence of a strong sibling effect (average ratio = 1.3), and because all behavioral observations were made after fledging, we used individuals as the unit of analysis.

We compared hourly calling rate between three age groups: 0–14, 15–28, and 29–42 days post-fledging; and a fledgling's distance from the natal nest over six age periods (0–15, 16–28, 29–52, 53–74, 75–97, and 98–137 days post-fledging). We tested whether the distance between siblings increased over three post-fledging age periods (0–37, 38–74, and 75–121 days). For analysis, we grouped fledgling ages differently because the data collected for calling, distance from the nest, and distance between siblings varied in quantity. We were able to collect data on distance from nest longer than any other measure. Also, calling rates were recorded hourly, unlike both distance measurements. The selected age groups fulfilled minimum sample size requirements for the most suitable statistical tests and to achieve a stratified distribution of data points (P. Chapman, pers. comm.). All data sets used for these analyses were log-transformed to equalize the variance of errors (SAS Inst. Inc. 1987; PC ver. 6.10) but the raw data are reported in this paper. The α level for all statistical tests was 0.05.

To analyze data on parent-offspring interactions, we used ANOVA (Proc GLM; SAS Inst. Inc. 1987; PC ver. 6.10) on log-transformed data to test whether calling rates or fledgling distance from the nest changed when parents were present. We also examined whether fledgling distance from the nest depended upon an interaction between parents' presence and fledging age.

RESULTS

Hourly calling rate.—The number of calls per hour did not change with time after fledging (Wilks' Lambda $F_{2,412}$ = 0.06, $P > 0.05$). The mean values for each of the three groups were similar, with an overall mean of 11.4 (± 0.01) calls hr ^{1} (Fig. 1). Calling rate did not differ between the sexes ($F_{1,413}$ = 0.50, $P >$ 0.05).

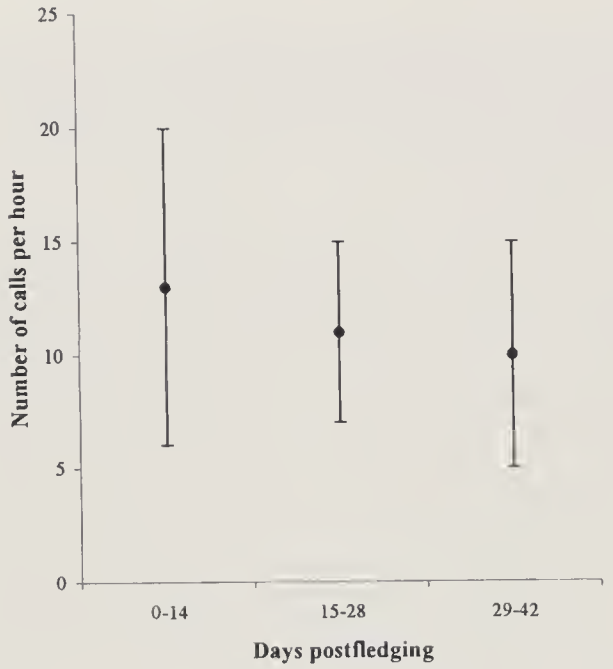

FIG. 1. Mean number of calls |SE| per hour for Golden Eagles in three post-fledging time periods (0–14, 15–28, 29–42 d) in the Little Missouri National Grassland of western North Dakota, 1993 and 1994.

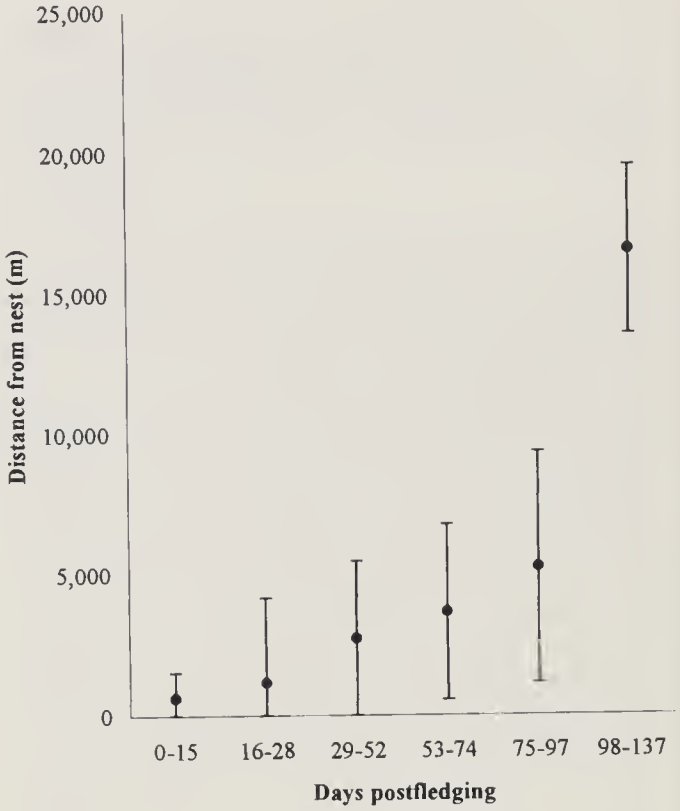

FIG. 2. Mean distance from the nest (m) |SE| for Golden Eagles in six post-fledging time periods (0–15, 16–28, 29–52, 53–74, 75–97, 98–137 d) in the Little Missouri National Grassland of western North Dakota, 1993 and 1994.

Distance from nest.—The distance of fledglings from their nests increased significantly with time (Wilks' Lambda $F_{4,10} = 11.53$, $P = 0.001$; Fig. 2) and eventually resulted in loss of radio contact within the study area (27,500 km^2) as the birds dispersed. There was no difference between sexes in the distance individuals dispersed ($F_{1,13} = 0.06$, $P > 0.05$).

Sibling interactions and juvenile behavior.—We collected data from six sibling pairs to determine the mean distance between siblings with time since fledging. There was no significant (Wilks' Lambda $F_{2,3} = 0.34$, $P > 0.05$) change over the time period of our study (Fig. 3).

Fledgling pairs frequently exhibited nonaggressive social behavior. Siblings often followed one another or flew together. We observed mutual preening or "nibbling" (Ellis 1979) when the fledglings perched together ($n = 288$), as they frequently did. We observed three different sibling pairs display "play" catching and plucking of prey together. We recorded no overtly aggressive social behavior between sibling pairs, and this social activity did not appear to change over time.

The mean age at first flight was 10.1 (± 0.08) weeks. We observed 11 attempts of prey capture by juveniles. Two of the observed at-

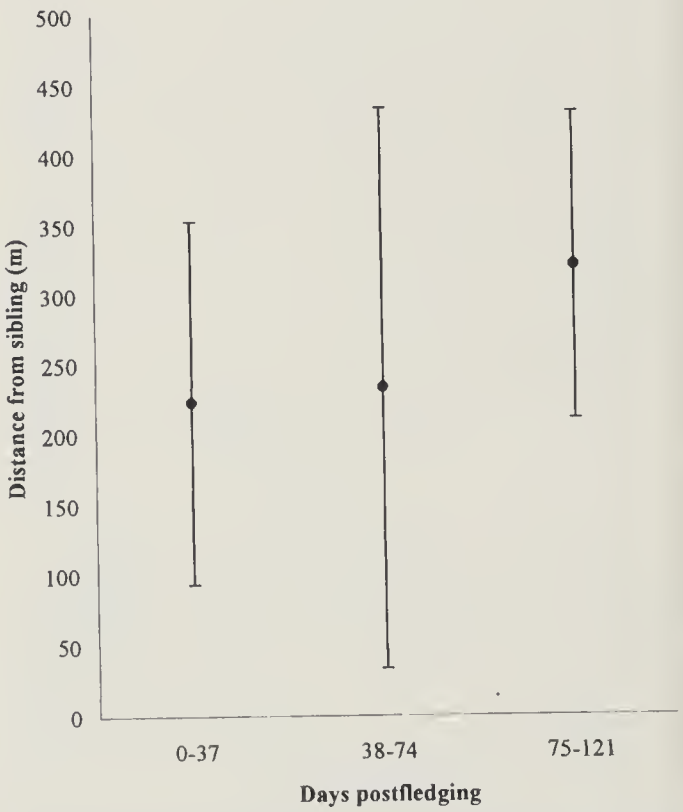

FIG. 3. Mean distance |SE| between Golden Eagle siblings (6 pairs) in three post-fledging time periods (0–37, 38–74, 75–121 d) in the Little Missouri National Grassland of western North Dakota, 1993 and 1994.

tempts were successful, with prey items including an unidentified snake and a rodent.

Parental interactions.—We observed parents near the focal bird relatively infrequently (29.6%) during observation periods. Calling rates of the young were higher in the presence of parents than when parents were not visible ($F_{1,413} = 14.39$, $P = 0.001$). The rate of calling nearly doubled for juveniles with a parent present ($\bar{x} \pm SE = 21.8 \pm 3.5$ calls hr^{-1}) versus parents absent (11.5 ± 1.7 calls hr^{-1}). Fledglings were closer to the nest when parents were present ($F_{1,13} = 10.81$, $P = 0.001$), but distance from the nest was not significantly correlated with the interaction of fledgling age and parental presence ($F_{4,10} = 0.96$, $P > 0.05$). We did not observe any aggressive behavior by the parent toward the offspring.

DISCUSSION

Calling rate did not change as the birds aged after fledging, although we observed a high degree of individual variation. A similar finding was reported in a Japanese population of Black Kites (*Milvus migrans*; Koga and Shiraishi 1994). Increased calling with age was reported in Spanish populations of Black Kites (Bustamante and Hiraldo 1990), the Egyptian Vulture (*Neophron percnopterus*; Ceballos and Donazar 1990), and the Spanish Imperial Eagle (*Aquila adalberti*; Alonso et al. 1987). The increased calling rates in these studies were attributed to a decrease in provisioning by parents as the young aged. Our results do not corroborate findings of increased calling with age. It is possible that food provisioning did not decrease over time in our study, resulting in no change in calling rates. It is also possible that food provisioning decreased, but calling did not increase because the young were becoming independent and beginning to hunt on their own. We cannot evaluate these hypotheses because we did not have enough data to analyze food provisioning rates.

Throughout our study, the appearance of a parent resulted in increased juvenile calling compared with when parents were absent. Increased calling in the presence of a parent is commonly observed in raptors (Alonso et al. 1987, Ikeda 1987, Hiraldo et al. 1989, Bustamante 1994a). Calling by juveniles may facilitate juvenile location by parents (Ikeda 1987). Calling also informs the parents of the nutritional status of their offspring (Trivers 1974).

Distance from the nest increased as the juveniles aged, probably in part due to increased flying proficiency. As independence nears, movements may not represent a linear dispersal, but may resemble "wanderings" outside the natal area. Similar observations have been reported for other species (Boeker and Ray 1971, Beecham and Kochert 1975, Steenhof et al. 1984, Walker 1987, Bahat 1992).

Siblings tended to move together after leaving the nest, and the distance between them remained relatively constant. This contradicts Newton's (1979) idea that fledgling raptors tend to perch apart. Other studies also revealed increased distance between siblings with age (Hiraldo et al. 1989, Bustamante and Hiraldo 1990, Ceballos and Donazar 1990). Increased sibling distance has been attributed to "tension" between juveniles or increased flight proficiency. Bustamante (1994a) reported that Kestrels (*Falco tinnunculus*) perched close together and engaged in social behavior similar to the young Golden Eagles we observed. Bustamante (1993) also found siblings of Black-shouldered Kites often perched together. Kenward and coworkers (1993) saw the same tendency with Northern Goshawk (*Accipiter gentilis*) siblings.

If parents and offspring were in conflict, resulting in the adults "driving-off" the juveniles, or if parents used aggression to evaluate the young's flight proficiency (Ferrer 1992), we should have observed agonistic interactions during the times when the parents were seen with the offspring, but we did not. Although parental aggression has been observed in raptor species (Robertson 1985, Alonso et al. 1987, Walker 1987, Hiraldo et al. 1989), it is often the case that the parents feed their offspring long after they have fledged (Ikeda 1987, Walker 1987, Bustamante and Hiraldo 1990, Ceballos and Donazar 1990, Bahat 1992).

We did not find an increase in aggression between siblings, as we predicted. Although juveniles moved away from their parental home range, they apparently remained together, indicative of sibling attraction rather than aversion. Our data do not support the predictions that an increase in parental and/or sibling

agression is associated with independence in this population.

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GROWTH PATTERNS OF HAWAIIAN STILT CHICKS

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ABSTRACT.—We studied chick growth and plumage patterns in the endangered Hawaiian Stilt (*Himantopus mexicanus knudseni*). Body mass of captive chicks closely fit a Gompertz growth curve, revealing a growth coefficient (K) of 0.065 day^{-1} and point of inflection (T) of 17 days. When chicks fledged about 28 days after hatching, they weighed only 60% of adult body mass; at 42 d, birds still were only 75% of adult mass; culmen, tarsus, and wing chord at fledging also were less than adult size. This trend of continued growth to adult size after fledging is typical for most shorebirds. After hatching, captive chicks grew more rapidly than wild chicks, probably because of an unlimited food supply. We found no evidence for adverse effects of weather on the growth of wild chicks. As with other shorebirds, the tarsus started relatively long, with culmen and then wing chord growing more rapidly in later development. Tarsal and wing chord growth were sigmoidal, whereas culmen growth was linear. We describe plumage characteristics of weekly age classes of chicks to help researchers age birds in the wild. *Received 28 Dec. 1998, accepted 20 April 1999.*

Avian growth patterns have been studied primarily because of their relationships to the ecology and evolutionary history of different species (Ricklefs 1968, 1973, 1983; O'Connor 1984; Anthony et al. 1991), and to maximize food yields of domestic animals (e.g., Anthony et al. 1991). Although there is selection for rapid independence of chicks, which should reduce variance in growth rates, intraspecific growth patterns can be variable and flexible because of environmental variability and competing selective pressures (Cooch et al. 1991, Emlen et al. 1991). In studies of wild birds, altricial species have been studied more often than precocial species, at least in part because the former remain in the nest from hatching until fledging.

In this paper we present information on chick growth patterns of the Hawaiian Stilt (*Himantopus mexicanus knudseni*), a precocial bird that is an endangered subspecies of the Black-necked Stilt. Like all shorebirds, stilts are precocial and nidifugeous. Hawaiian Stilts are significantly larger than the nominate race (Coleman 1981) and differ somewhat in adult plumage characteristics (Wilson and Evans 1893, Coleman 1981). Stilts are found on all five major islands in Hawaii, breed exclusively in shallow, lowland wetlands (USFWS 1985), and statewide population counts indicate a steady increase in population size (Reed and Oring 1993). Our specific objectives were to (1) describe patterns of Hawaiian Stilt chick growth from captive and wild birds and compare them to other shorebirds, and (2) provide a method for aging chicks in the field. The last objective was designed for studying preadult mortality patterns by providing aging criteria that do not requiring capturing the bird.

METHODS

Captive birds.—Growth data for captive birds came from 15 individuals raised from eggs in 1980 in the Honolulu Zoo. Because chicks were kept in a common enclosure, some competition for food might have occurred, although food was provided *ad libitum*. Because all birds were subject to the same feeding and environmental conditions, inter-individual variability in growth should be minimized. All birds were weighed daily for 42 days to the nearest 0.1 g. Hawaiian Stilts fledge approximately 28 d after hatching (Coleman 1981).

One of the 15 birds was used only for the first 13 d because a bill deformity developed at this time, caus-

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ing the individual to lose mass quickly. A sixteenth bird was not included in the analysis because of aberrant fluctuations in growth. Its mass at hatch was over 5 standard deviations above the mean, and it gained mass rapidly for 11 days. Between days 12–17, however, it lost 25% of its body mass, dropping well below the mean (ca 2 standard deviations); on day 18 it began to grow rapidly again, reaching mean mass for the group 24 d later.

Other variables (culmen, tarsus, and wing chord) were measured less regularly. Measurements were made every 2–4 d after hatching and became less frequent (every 4–10 d) after fledging. Some individuals were measured more often than others. Despite this variation, we were able to derive useful growth patterns for these body measurements. Mass was measured by one person and lengths by another.

A growth curve for body mass was fit to a Gompertz equation (r^2 = 0.99; SPSS, Inc. 1995, NONLIN procedure) because it is used most often for shorebirds (e.g., Beintema and Visser 1989a) and we wanted to allow interspecific comparisons to be made (O'Connor 1984). The fit was made on average values for each day from 12–15 individuals. The Gompertz equation has the form

$$W = A \times e^{-e^{-Kt}}$$

where W is body mass (g), A is asymptotic (adult) mass (g), K is the growth coefficient (day^{-1}), t is age (d), and e is the base for natural logarithms. Adult mass came from 43 adult males and 42 adult females (Coleman 1981). Although adult females weigh slightly more than males (mean difference = 7.0 g), the difference is a small percentage (<4%) of total body mass, consequently A was averaged across sexes (202.5 g).

Wild birds.—Wild chicks were captured by hand on the islands of Oahu, Maui, and Kauai in 1978–1980 and 1993. During 1978–1980, we captured chicks with known hatching dates 142 times. Because chicks from the same clutch were not considered to be independent, they were averaged within each clutch (maximum of four chicks averaged per clutch). This resulted in 33 measurements of chicks less than 24 h old (designated day 0; n = 64 chicks). Chicks were remeasured every time they were encountered and captured. This resulted in 43 measurements of birds from 2–32 d old (n = 78 chicks). We measured mass to the nearest 1.0 g, culmen and tarsus lengths to the nearest 0.1 mm, and wing chord to the nearest 1.0 mm. In 1993, we took measurements on 55 birds ranging in age from hatching to fledging using the above methods. During 1993 we rarely knew the exact age of each chick, so these measurements were used only to determine the relationships among body measurements. Tarsus and wing chord measurements were made on the right side of the chick and the same person made all measurements in 1993. We also noted the presence or absence of an egg tooth. Field measurements from 1978–1980 were made by one person, and in 1993 by another, so values were not compared.

Plumage.—We considered only those plumage characteristics that were visible in the field: fuzzy appearance associated with down, brown versus black cast, presence of an eye ring, etc. We used the above characteristics to describe plumage of weekly age classes. In several cases, plumage descriptions for weekly age classes were incomplete (e.g., lacking description of wing coloration for week 3). Because plumage is essentially the same for chicks of both Hawaiian and Black-necked stilts (Coleman 1981), we supplemented our descriptions of Hawaiian Stilts with plumage observations of wild, known-aged Black-necked Stilt chicks at Honey Lake, California in 1997. Plumage of adult Hawaiian Stilts is different from fledglings (Robinson et al., in press).

Analyses.—Statistical analyses were conducted using version 7.0 of SPSS (SPSS, Inc. 1995). One assumption in comparing body measurements between captive and wild birds is that initial body sizes are equal. To test this, we used multiple analysis of variance (MANOVA) to compare mass and culmen length, tarsus and wing chord measurements between known-aged captive and wild hatch day (day 0) birds. For ages after day 0, we determined whether or not mean values for wild birds fell within 95% confidence intervals for mean values of captive birds. All statistical tests were two-tailed. Values presented are means ± SD.

RESULTS

Growth in captivity.—Growth parameters for the Gompertz equation indicated a growth coefficient (K) of 0.065 and time to inflection point (T) of 17 days. Although chick mass varied little among the 11 individuals on day of hatch (15.7 ± 0.6 g), variability in mass among individuals increased greatly over the first two weeks (60.4 ± 9.2 g), and remained high up to fledging at day 28 (122.5 ± 10.6 g). In general, differences among chick mass at day 14 are consistent until fledging, indicating that chicks that gain relatively more mass in the first two weeks after hatching tend to fledge at a heavier mass than chicks that gain less mass their first two weeks. Captive individuals did not experience a significant mass loss between day 0 (hatch day) and day 1 (paired t-test: t = −0.432, df = 10, P > 0.05).

At fledging, chicks had not attained adult body mass or body measurements. Mass at fledging was 60% of adult mass, culmen length was 67% of adult length, tarsus length was at 66%, and wing chord length was at 55% (adult measurements from Coleman 1981).

Growth in the wild.—There was no differ-

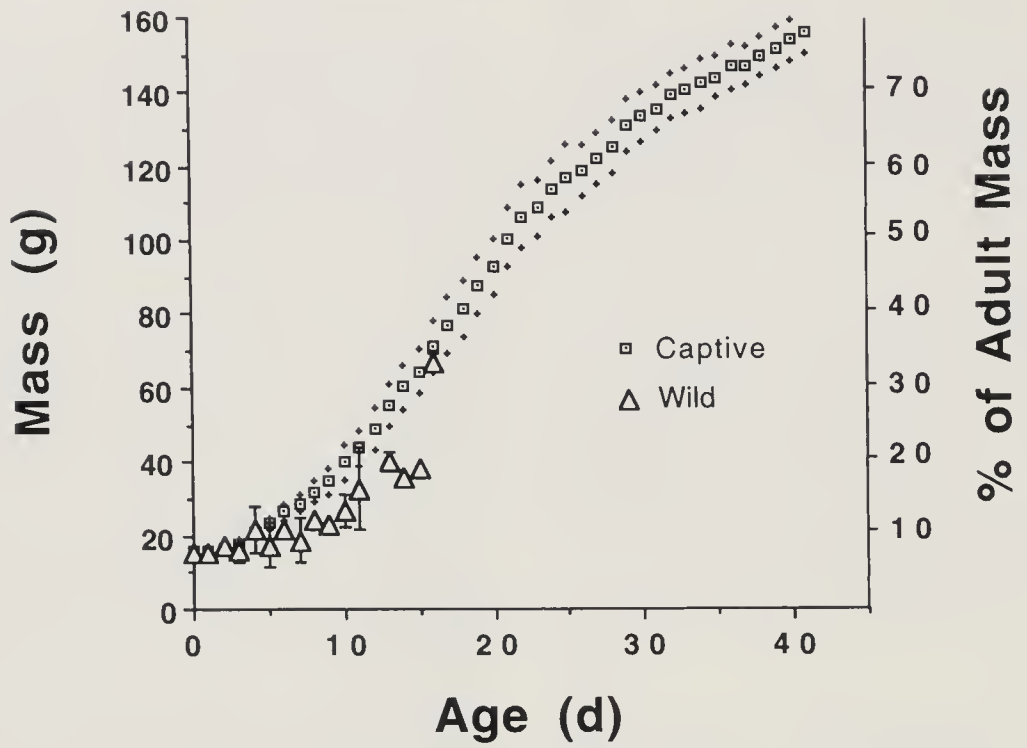

FIG. 1. Captive and wild Hawaiian Stilt chick mass and percentage of adult body mass (202.5 g) as a function of age. Values are means ± SE.

ence between mean mass of captive ($\bar{x}$ = 15.7 ± 0.6 g) and wild ($\bar{x}$ = 15.6 ± 1.1 g) chicks at hatch (t = 0.551, df = 40, $P > 0.05$). The apparent decrease in mass between day 0 (hatch day) and day 1 for wild chicks was not significant (paired t-test: t = 0.585, df = 12, $P > 0.05$). From days 1 to 17, masses of same-aged wild birds typically fell within the 95% confidence interval of captive birds, though below the mean. In three comparisons (day 9, 14, 15), the mass of wild birds fell below the 95% confidence interval for captive mass. Mass gain with age generally followed a sigmoidal pattern, with individuals not reaching an asymptote until after 42 days of age (Fig. 1). Similarly, from days 1 to 17, mean wing chord of same-aged wild birds fell within the 95% confidence interval of captive birds, with the exception of days 9, 14 and 15, when mean wing chord measurements for wild birds fell below the 95% confidence interval. Growth of the wing chord also followed a sigmoidal pattern, although the slope of the curve was less steep for wing chord growth than it was for mass gain (Fig. 2). Mean culmen length and mean tarsus length did not differ between wild and captive birds from days 1 to 17. Mean culmen growth for both wild and captive chicks was relatively linear with increasing age (Fig. 2).

Relative growth rates.—Relative growth rates among different parts of the body can be assessed without reference to age. We found tarsus length to be long in early development relative to culmen and wing chord, and it continued to grow at a faster rate than the culmen throughout development. Culmen and wing chord grew at approximately the same rate in early development until wing chord reached about 40 mm; as wing chord continued to grow, culmen length growth rate slowed considerably. Changes in wing chord and body mass were similar throughout the growth period observed (Fig. 3). Changes in tarsus length and body mass also were similar until individuals reached approximately 80 g, when tarsus growth slowed.

Plumage.—Using field data from known-aged chicks, we constructed a table of weekly plumage characteristics for Hawaiian Stilt chicks (Table 1). The presence or loss of down, as well as overall body color, appear to be the two best indicators of chick age in the wild for weeks 1–3. Aging during this time is more precise if one can determine the presence and condition of primary sheaths; this cannot be done, however, without chicks in hand. Specifically, in week 1 chicks are entirely covered with down, and primary sheaths are absent. The dorsal surface of the body in-

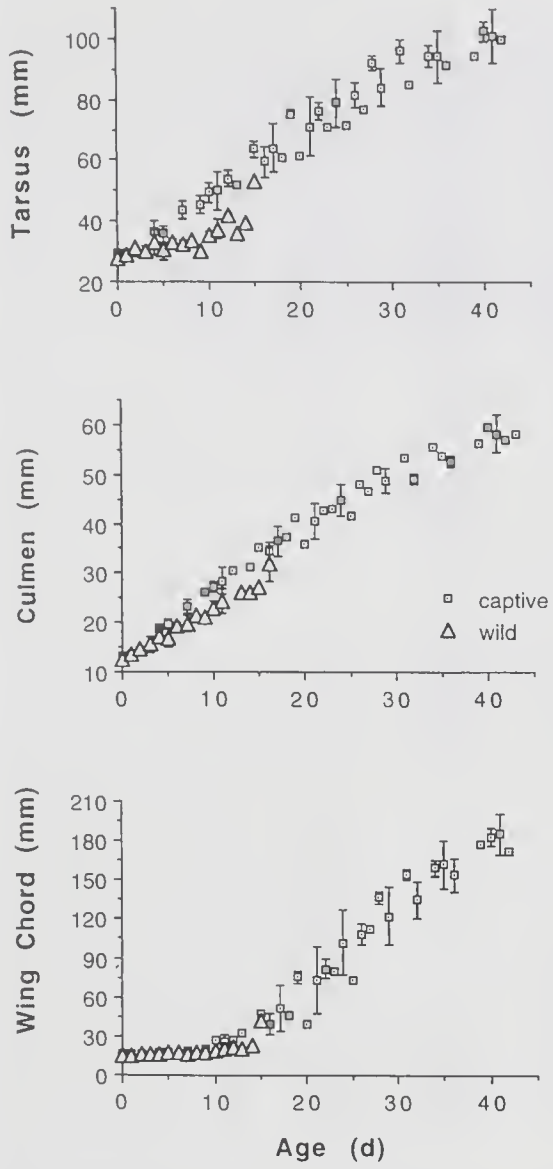

FIG. 2. Growth patterns for wing chord, culmen length, and tarsus length of captive and wild Hawaiian Stilt chicks.

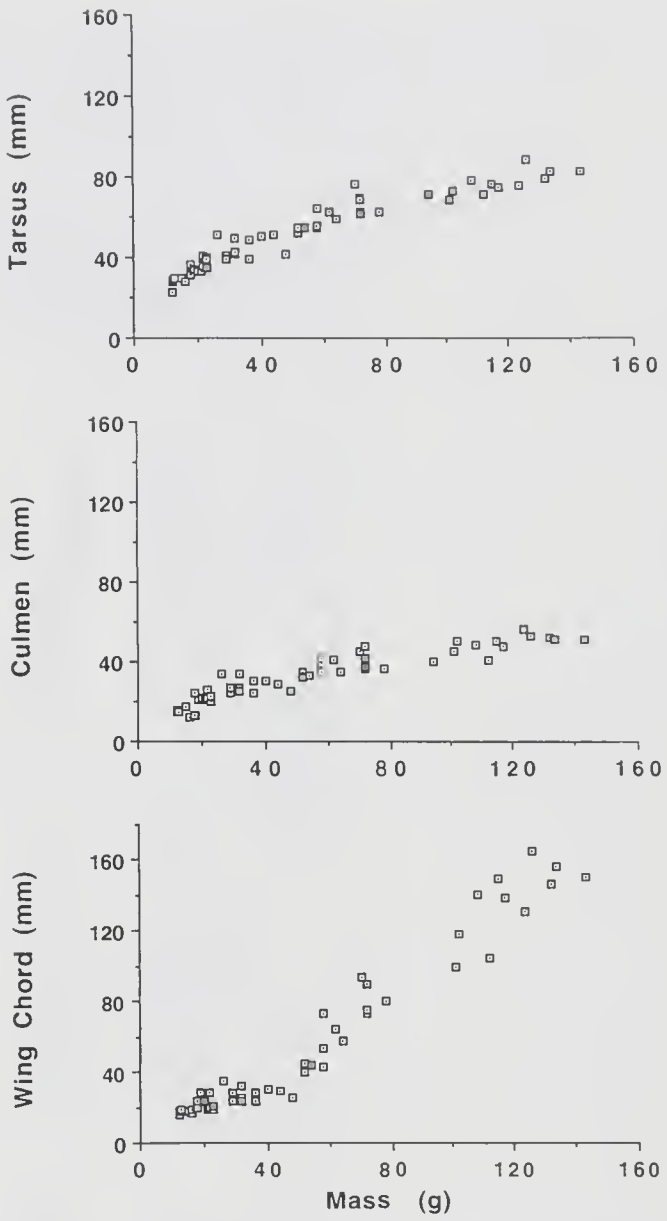

FIG. 3. Relative growth rates of three body measurements of wild Hawaiian Stilt chicks compared to body mass.

cluding head, neck, back, and wing is mottled black, golden brown, and white; the ventral surface is creamy white. In week 2, the head begins to turn brown and is distinctly lighter than the rest of the body. Mottling on the neck changes to a more solid pattern of gray and tan. Most importantly, primary sheaths emerge on day 12. During week 3, down begins to disappear, giving chicks a sleeker appearance. Overall body coloration changes from mottled black, golden brown, and white to plain gray and white, and primary sheaths are broken about day 16. In all cases where we had information on both subspecies, plumage descriptions of known-aged Black-necked Stilt chicks matched exactly the plumage descriptions of known-aged Hawaiian Stilt chicks up to and including six weeks of age.

From 4–6 weeks, age classes can be differentiated by the presence of tail feathers, the ability to fly, and the presence of an eye patch and eye ring. In week 4, tail feathers emerge and the eye patch and eye ring become visible. During week 5, all down is lost, wing feathers are fully developed enabling short distance flight (up to 1.5 m), and the eye patch is distinct. Finally in week 6, chicks are capable of prolonged flight.

As with other shorebirds (Clark 1961), the egg tooth typically was lost after the first day and always was gone after 48 h.

DISCUSSION

Because shorebird chicks feed themselves, they hatch with well developed legs and a

TABLE 1. Plumage characteristics of wild Hawaiian Stilt chicks according to weekly age classes.

	Down	Overall body color	Head	Neck	Back
Week 1	Covers entire body	Dorsal mottled black, golden brown & white; Ventral white	Dorsal mottled black, golden brown & white; Ventral creamy white	Dorsal mottled black, golden brown & white; Ventral creamy white	Contours ~day 5; mottled black, golden brown & white
Week 2	Covers entire body	Dorsal mottled black, golden brown & white; Ventral gray to creamy white	Beginning to turn brown; lighter than rest of body	Dorsal gray & tan; Ventral creamy white	Mottled black, golden brown & white
Week 3	Beginning to lose; Some on head, lower neck & upper back; tail downy	Gray & white from distance	Dorsal brown; Ventral creamy white	Dorsal gray; Ventral creamy white	Mottled black & golden brown
Week 4	Some remaining on head, at base of secondaries & at tips of tail feathers	Black & white from distance	Black on top; otherwise brown	Dorsal gray; Ventral creamy white	Mottled black & golden brown
Week 5	None	Black & white	Mostly black w/brown flecks	Dorsal gray; Ventral white	Mottled black & golden brown
Week 6	None	Black & white	Mostly black w/brown flecks	Dorsal gray; Ventral white	Mottled black & golden brown

TABLE 1. EXTENDED

	Wing	Tail	Primary sheaths	Secondaries	Humeral tract	Eye patch	Eye ring
Week 1	Mottled black & golden brown w/white perimeter	Black w/golden brown tips	Not present	Not present	Not present	Not present	Not present
Week 2	Mottled black & golden brown w/white perimeter	Black w/golden brown tips	Present ~day 12	Slightly brown	Brown	Not present	Not present
Week 3	Mottled black & golden brown w/gray leading edge	Black w/golden brown tips	Broken ~day 16	Mottled black & brown	Brown	Not present	Not present
Week 4	Mottled black & golden brown w/gray leading edge	Feathers present for first time	In broken sheaths	Brown	Brown	Just visible; white	Present & black ~day 25
Week 5	Fully developed; can fly short distances (5′); black w/brown tips	Fully feathered; Black w/golden brown tips	In broken sheaths; Free & molt complete ~day 33	Brown	Brown	Distinct; white	Present; black
Week 6	Flying	Black w/golden brown tips	Not present	Brown	Brown	Distinct; white	Present; black

partly developed bill; wing development begins later and is rapid once started (Galbraith 1988, Thompson et al. 1990). Growth patterns are variable among species (Holland and Yalden 1991; Starck and Ricklefs 1998a, b). For example, body mass at fledging as a percentage of asymptotic adult body mass varies in shorebirds (Scolopacidae and Charadriidae) from 53% to 91% (Beintema and Visser 1989a). In addition, it has been suggested that shorebirds have a higher growth coefficient (K) than other terrestrial, precocial birds (Beintema and Visser 1989b). Of 15 species reviewed by Beintema and Visser (1989a), K ranged from 0.051 to 0.158, and the inflection point (T) ranged from 5.5 to 23.8 d after hatch. Not surprisingly, body size is positively correlated with the inflection point and negatively correlated with the growth coefficient. That is, larger species reach the half-way point in growth at a relatively larger size, and grow at a slower rate in proportion to their adult body size, than do smaller species. Hawaiian Stilts conform to these patterns.

Shape of growth curves.—Captive Hawaiian Stilt chicks grew from approximately 15 g at hatching to 125 g at fledging, attaining only 60% of adult body mass when they fledged. Culmen, tarsus, and wing chord also were still growing at fledging, well below adult sizes, and did not reach adult values until after 42 days after hatching. Culmen and tarsus sizes increased rapidly between hatching and fledging, with culmen growth generally following a linear trajectory and tarsus following a slightly sigmoidal pattern. Wing chord growth was sigmoidal, with slow growth from hatch day to day 12 followed by a substantial increase in growth rate when chicks reached 13–15 days old.

Mass loss in the first 24–48 h after hatch has been reported in some shorebird species (e.g., Lapwing, *Vanellus vanellus*; Galbraith 1988) and is attributed to movement away from the nest cup soon after hatching. Although Hawaiian Stilts also leave their nest cup within a day of hatching, we found no significant mass loss for captive or wild chicks from day of hatch to day 1. Differences in the distance traveled and the amount of food available in the first 24 h may explain interspecific and intraspecific differences in shorebird mass loss immediately after hatching. Reasons for variation in shorebird post-hatching mass loss require further investigation.

Comparison of captive and wild chick growth.—Captive and wild chick masses did not differ significantly for most ages; when they differed, wild birds were lighter than captive birds. By the end of week 1 captive chicks generally were growing at a faster rate than wild chicks for all growth parameters measured. This trend mirrors results from other studies of precocial birds (Beintema and Visser 1989a). In most cases, captive and wild chicks have similar growth curves, with more variation in the growth of wild chicks (Visser and Ricklefs 1993). Faster growth in captivity could be due to an unlimited food supply, while slower growth in the wild could be attributed to colder weather, which increases the costs of thermoregulation and reduces the amount of time that chicks can spend foraging. A study of time budgets in the field of three precocial charadriiform species revealed that during adverse weather, young chicks were brooded for 75% of the daytime, and as a result, they could not obtain enough food to satisfy their energy requirements (Beintema and Visser 1989a). In contrast, during good weather conditions, chicks foraged almost continuously once they were able to thermoregulate.

Beintema and Visser (1989a, b) hypothesized that for shorebird species, cold temperatures and cold with rain are the main causes of slower chick growth in the wild. Specifically, temperatures dropping below 15° C slowed chick growth. In Hawaii, temperatures in coastal wetlands where Hawaiian Stilts breed rarely fall below 21° C, and there are no records of temperatures as low as 15° C. In addition, rains at coastal areas typically are short-lived. The fact that growth was slower in wild chicks despite temperatures above 15° C suggests that temperature itself is not the main factor affecting slower Hawaiian Stilt chick growth in the field. At warmer temperatures, Pierce (1986) observed faster growth in other stilt species. Either a different threshold applies to Hawaiian Stilts or differences were due to food availability (Beintema 1994).

Comparison to other species.—Hawaiian Stilts grow slowly in comparison to other shorebirds. Of the 42 growth coefficients

Starck and Ricklefs (1998a) reported for 27 species of shorebird, only 5 were lower than what we calculated for Hawaiian Stilts, and all came from heavier species. The only published estimates of *Himantopus* growth coefficients are Starck's and Ricklefs' (1998a) calculations from Pierce's (1986) data on Pied (*Himantopus himantopus leucocephalus*) and Black (*H. novaezealandiae*) stilts. These species have lower adult masses (129 g and 130 g, respectively) than do Hawaiian Stilts, but do not fledge until a later age. Hawaiian Stilts fledge approximately 28 days after hatching; Pied Stilt chicks do not fledge until they are 34 d, and the Black Stilt fledges even later (at 46 d; Pierce 1986). Similar to the Hawaiian Stilt, both species continue to grow after fledging. However, based on data presented by Pierce (1986: fig. 6), Pied and Black stilts fledge at a higher percent of their adult body mass. Consequently, despite the longer time to fledging, Pied and Black stilt growth coefficients are consistent with expectations based on their adult size (K = 0.175 and 0.129 respectively; Starck and Ricklefs 1998a). A K of 0.074 would be expected for the 202.5 g Hawaiian Stilt (Beintema and Visser 1989a), but we observed K = 0.065 for Hawaiian Stilts in captivity (and possibly lower in the field; Fig. 1). Starck and Ricklefs (1998a) also reported faster growth coefficients for the European Avocet (*Recurvirostra avosetta*; K = 0.213 and 0.171 from two different studies), which is similar in mass to Hawaiian stilts (168 g and 250 g, respectively). Although the relationship between body mass and K in Charadriiformes, is poor (r^2 = 8%, n = 75 species; Starck and Ricklefs 1998b), these data demonstrate that the slow growth rate observed in Hawaiian Stilts is not a characteristic of the Recurvirostridae.

We do not know why Hawaiian Stilts have slow growth. The two obvious hypotheses do not provide satisfactory explanations. First, growth rate could be correlated with latitude. Tropical environments provide a longer breeding season, and growth rates of tropical altricial species are lower than are those of taxonomically related temperate species (Ricklefs 1976, Oniki and Ricklefs 1981). The Hawaiian Stilt breeding season lasts six months (Coleman 1981). Despite this, neither the incubation nor fledging period is prolonged. Worldwide, stilts average 22–26 days of incubation (Johnsgard 1981), which incorporates the Hawaiian Stilt's incubation length of 25 days (Colemen 1981). As noted above, the fledging time is shorter in this species than in others of its genus (Johnsgard 1981, Pierce 1986) so there is no extended time as a chick. There are no studies of which we are aware comparing growth rates of precocial species across a latitudinal gradient, but it would be an interesting assessment.

Second, the lower growth rate could be a consequence of evolving in an island environment where predation rates might have been relatively low before human occupancy, and selection for rapid growth might have been relaxed. Most recorded mortality of adult Hawaiian Stilts is attributed to introduced species (Woodside 1979). However, one would expect slower growth to be associated with an older age at fledging, which does not occur. In contrast, the Hawaiian Stilt fledges at a smaller percent of adult body mass than do other stilts, resulting in an extended post-fledging growth period.

Estimating age.—Ideally, estimates of chick age would be based on a trait that changes rapidly and monotonically throughout growth. One problem with this method is that often no one trait is ideal throughout the entire growth period. Rather, traits differ in their accuracy for aging as chicks become older. For example, measurements of tarsus and wing chord for Hawaiian Stilts are not useful for aging chicks at early and late ages because of their sigmoidal growth patterns. Using mass as an indicator of chick age is problematic because it fluctuates rapidly, depending on environmental conditions and when chicks are weighed in relation to their last feeding. For Hawaiian Stilts, culmen length may be the most useful parameter for aging chicks because its growth trajectory is fairly linear. Because it typically has a constant growth rate throughout the chick stage, culmen length has been used to age chicks of other shorebird species in the wild (Beintema and Visser 1989a). However, even for traits that tend to vary linearly and monotonically throughout development, there is a tremendous amount of individual variation in daily growth. Unfortunately, this individual variation is magnified by measurement error when all measurements

are not made by the same person. Thus, determination of chick age using body measurements and mass, regardless of the species, should be viewed as approximate at best.

As a result, we decided to describe general plumage patterns for Hawaiian Stilt chicks of known age in the field to set up criteria for establishing weekly age classes for chicks, defined by the presence or absence of specific plumage characteristics. The ability to identify approximate chick age in the field without capturing young of this endangered species could aid in management by helping to identify the age at which chicks disappear. To this end, we found definitive differences between plumage characteristics of specific age classes of Hawaiian Stilts. This should increase abilities to assess survival, the least understood life-history component of this species (Reed et al. 1998).

We found plumage characteristics to be useful for identifying weekly age classes of Hawaiian Stilts. Because culmen length is similar for captive and wild chicks and has a linear positive relationship with age throughout development, a combination of culmen length and plumage description may be the most accurate way to age wild Hawaiian Stilt chicks. Relying primarily on plumage characteristics, specifically because they are non-invasive, and supplementing these observations with culmen lengths if chicks are captured, will help minimize interference in this endangered species while providing managers with a tool for monitoring reproductive success and population numbers. Because adults and fledglings differ in plumage patterns, it also will allow accurate monitoring of reproductive success before molt.

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NESTING BEHAVIOR OF THE LILAC-CROWNED PARROT

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ABSTRACT.—Nesting behavior of the Lilac-crowned Parrot (*Amazona finschi*) was observed over a three year period at 24 nests in the tropical dry forest of the Chamela-Cuixmala Biosphere Reserve, western Mexico. Nest site characteristics and the pattern of parental care throughout the nesting cycle are described for this mainland Amazon parrot and compared with that reported for other Amazon parrot species. Nest sites were located in natural cavities of large mature trees characteristic of semi-deciduous forest. Nest sites were similar to one another in tree species, tree size, cavity height, and entrance width, indicating that Lilac-crowned Parrots may select nest sites based on these characteristics. Unlike most parrot species, Lilac-crowned Parrots showed low nest site reuse and high synchrony of nest initiation. Throughout the nesting cycle, females and nestlings were fed only twice a day on average. Nest attendance during feeding visits was short. The infrequent feeding visits and short nest attendance exhibited by Lilac-crowned Parrots corresponds with that found for other mainland Amazon parrots in northeastern Mexico, but contrasts with the multiple feedings and longer nest attendance observed for island Amazon species. The distinct aspects of Lilac-crowned Parrot nesting behavior may be related to predation rate and food resource availability during the extreme dry season. *Received 10 March 1999, accepted 15 July 1999.*

Most studies on the ecology of Neotropical Amazon parrots have been conducted on species inhabiting the Caribbean Islands (Snyder et al. 1987, Gnam 1991, Gnam and Rockwell 1991, Wilson et al. 1995). A comparative study of three species of mainland Amazon parrot in north-eastern Mexico found distinct differences compared with island species in some aspects of reproductive behavior and productivity (Enkerlin-Hoeflich 1995). Females and nestlings of three mainland Amazon parrot species were fed only twice a day (Enkerlin-Hoeflich 1995), in comparison with the multiple feedings observed for Caribbean Amazons (Snyder et al. 1987, Gnam 1991, Wilson et al. 1995) and other Neotropical parrots (Lanning 1991, Waltman and Beissinger 1992). Additional data on mainland Amazon parrots are needed to determine whether conclusions from studies on island species are applicable to mainland species. The Amazon parrot species of Mexico are particularly suited for comparison with the *Amazona* species of the Greater Antilles in the Caribbean because of their close evolutionary relationship (Snyder et al. 1987, Forshaw 1989). The Lilac-crowned Parrot (*Amazona finschi*) is endemic to western Mexico and has a restricted distribution from southeastern Sonora to Oaxaca (Forshaw 1989). There have been no studies on the ecology of the Lilac-crowned Parrot, and little is known of its breeding biology (Forshaw 1989). Anecdotal reports from captive breeding give an incubation period of 28 days, with the young chick leaving the nest after 60 days (Mann and Mann 1978). In this paper we present observations on the nest site requirements and nesting behavior of the Lilac-crowned Parrot in the wild, and compare them to observations for other island and mainland Amazon parrots.

STUDY AREA AND METHODS

Studies on the breeding biology of the Lilac-crowned Parrot were conducted at the 13,142 ha Chamela-Cuixmala Biosphere Reserve (19° 22′ N, 104° 56′ W to 19° 35′ N, 105° 03′ W) on the Pacific coast of Mexico. The study site has a dry tropical climate exhibiting a marked seasonality in precipitation, with 80% of the 748 mm average annual rainfall occurring June to November, and a prolonged drought from mid-February to late May (Bullock 1986). The reserve has a hilly topography varying in elevation from 20–520 m above sea level. The dominant vegetation type on the slopes is tropical dry deciduous forest, with semi-deciduous forest in the larger drainages and more humid valleys (Lott et al. 1987, Lott 1993). Monospecific forests of *Celaenodendron mexicanum* also occur as discontinuous patches within the tropical deciduous forest mosaic (Martijena and Bullock 1994).

Observations on the nesting behavior of Lilac-crowned Parrots were conducted from January to June in 1996–1998. Nest searches were carried out in Feb-

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TABLE 1. Cavity dimensions for 26 Lilac-crowned Parrot nests.

Nest character	Mean	Standard deviation	Range	Coefficient of variation (s/m) × 100
Tree diameter at breast height (cm)	43.1	11.4	27.7–66.3	26.3%
Cavity height from ground (m)	9.7	1.7	7.4–14.7	17.8%
Entrance width (cm)	10.0	2.3	6.4–14.0	22.5%
Entrance length (cm)	21.0	16.0	7.5–71.6	76.2%
Internal diameter (cm)	19.9	6.8	10.5–35.0	34.3%
Cavity depth (cm)	66.2	51.7	24–260	78.1%
Circumference at entrance (cm)	86.7	30.0	26–135	34.5%
Nearest active nest (m)	948.9	707.7	25–2419	74.6%

ruary during the nest prospecting and early incubation phases of the parrot breeding cycle. No additional nests were located later in the nesting cycle because the behavior of breeding pairs made detection of nest sites difficult. A cavity was considered a potential nest site if one or both of the adult parrots were observed entering it. The cavity was considered an active nest site if one of the adult parrots remained within the cavity for longer than 30 min. Nest site reuse was determined from the frequency of cavity occupancy between years.

Access to nest cavities was achieved using both single-rope ascending (Perry 1978, Perry and Williams 1981) and a tree bole climbing technique (Donahue and Wood 1995). Nesting requirements of the Lilac-crowned Parrot were determined by measurement of nest cavity dimensions: tree species, diameter at breast height (DBH) of the tree, height above ground of the entrance, width and length of entrance, cavity depth, internal diameter, and circumference of the tree at entrance (Saunders 1979, Saunders et al. 1982). The location of each nest site and where possible the tree used by the nesting pair for the transfer of food from the male to the female were obtained using a geographic positioning system. The coefficient of variation was determined for the mean cavity dimensions to evaluate the variability of characteristics between nest sites.

Behavior of breeding pairs was determined by observations of parrot nests from covered blinds using 10 × 40 binoculars. Continuous dawn to dusk observations were conducted on 30 man-days (360 hours) at 8 nests. No activity was observed at nests during mid-day; therefore additional observations were restricted to the first four hours after sunrise and the last three hours prior to sunset giving an additional 299 hours of observation at 16 nests. Parental care and investment was evaluated from the number of feeding visits to the nest, arrival time, duration of feeding visit, time spent in the nest cavity, and time spent in the nest area (defined as within 100 m of the nest). Descriptive statistics are presented with means, ranges, and standard deviations.

RESULTS

Nest site characteristics.—A total of 29 nest sites were located in 1995–1998, all of which occurred in natural cavities. Nest cavities were located in live trees of *Celaenodendron mexicanum,* local name Guayabillo (51.7%, $n = 15$), and *Astronium graveolens,* local name Culebro (31.0%, $n = 9$). Of the remaining 5 cavities, 2 were located in a *Tabebua* species, 1 was located in a dead tree, and 2 were located in unidentified trees. Nest site reuse was low, with only 3 (10.3%) of the 29 nests sites located between 1995 and 1998 being used by nesting pairs over more than one breeding season. One cavity was used in three of the four years; 1995, 1997, and 1998. Two other cavities were reused once after a vacancy of one year.

Mean cavity dimensions for 26 active nest sites are presented in Table 1; three cavities could not be accessed for safety reasons. The cavity dimensions with the least variation were height of entrance from the ground and width of entrance. Diameter of tree at breast height was relatively consistent between nest sites and reflects the fact that parrot nests were located in large, mature trees characteristic of semi-deciduous forest. The greatest variability was found in depth of cavity and length of entrance.

Egg-laying and incubation.—Timing of egg-laying was highly synchronized between nests with most pairs commencing incubation within 14 days of the first nest being initiated. Mean nest initiation date was 6 February ± 4.6 (SD) days in 1996 (range: 30 January–13 February, $n = 8$), and 15 February ± 5.3

days in 1997 (range: 10–23 February, n = 6).

Nest attendance by the female was high during incubation, with the female leaving the nest only once in the morning and once in the afternoon to be fed by the male. The female spent a mean of 39.4 ± 26.5 min per day out of the nest over both morning and afternoon feeding sessions (range: 15–95 min per day, n = 20). Conversely, the male was rarely observed entering the nest or perching on the nest rim. Daily activity periods were consistent between nests with the male making an average 2.1 ± 0.3 nest visits per day (range 2–3 visits, n = 35) to feed the female. Mean arrival times for the morning and afternoon activity periods were respectively 08:24 EST ± 46 min (range: 06:07–10:08, n = 45) and 18:14 EST ± 26 min (range: 17:15–19:03, n = 40). Each feeding visit by a male lasted an average of 33.9 ± 25.6 min (range: 5–113 min, n = 80).

The male usually vocalized loudly on his approach to the nest area and perched in a tree adjacent to the nest cavity making low contact vocalizations until the female emerged. The nesting pair gave a characteristic take-off squawk, or bugle, as the female flew from the nest cavity to join the male. Food transfer from the male to the female took place in a regular perch tree located an average 423 ± 228 m (range: 149–983 m, n = 11) from the nest cavity. The food transfer session was the only time during the incubation phase when both adults were away from the nest area and was short in duration (average 11.5 ± 10.4 min, range: 2–48 min, n = 78).

Parental care.—Eggs hatched asynchronously, and females continued to brood nestlings during the day until the oldest nestling was 19.6 ± 2.7 days old (range: 15–23 days, n = 9). Females ceased roosting in nests overnight when the youngest chick was in its third week. During this early nestling phase, the male continued to feed the female twice a day and was occasionally observed to enter the nest for a mean 1.7 ± 2.8 min (range: 0–8 min, n = 9) per feeding visit. Later in the nesting cycle when the chicks were larger, both parents entered the nest to feed the young.

The behavior of nesting pairs altered once the female began to forage with the male. Nesting pairs became more secretive around nests, arriving and departing silently. Pairs used low, almost inaudible vocalizations when in the nest area. Pairs were cautious about approaching the actual nest, and would not do so if they detected an observer or another disturbance. The nesting pair made an average 2.6 ± 0.9 visits per day (range: 2–4 visits, n = 25) to feed the nestlings. Average duration of feeding visits during the nestling phase was 72.3 ± 42.3 min (range: 12–171 min, n = 31). However, the nesting pair spent the majority of this time perched in trees around the nest area. Attendance at the actual nest cavity was short, lasting an average of 10.6 ± 11.2 min [range: 1.0–27.2 min, n = 30 (total time either adult in nest cavity or at entrance)], with a mean of 5.4 ± 4.5 min per visit (range: 0–17 min, n = 30) spent within the nest cavity, and a mean of 6.0 ± 12 min (range: 0–20.6 min, n = 30) perched at the nest rim. Each adult spent a mean of only 4.0 ± 3.5 min (range: 0.42–17 min, n = 41) inside the nest cavity per feeding visit. This was sufficient time to feed the young; however, there was no indication that parent birds spent any other time in the nest with the young except when feeding them.

Prior to fledging, nestlings began to climb to the nest entrance, and were fed at the nest rim. During this stage, nesting pairs spent more time perched near the nest entrance making low contact vocalizations to the young. Mean age at fledging was 63.7 ± 3.2 days (range: 56–68 days, n = 22). Nestlings fledged asynchronously, and all nests fledged young within a 2–3 week period. All nestlings fledged within 12 days in 1996 (mean fledge date = 10 May ± 4.34 days, range: 6–18 May, n = 8), 17 days in 1997 (mean fledge date = 18 May ± 6.68 days, range: 11–28 May, n = 7), and 13 days in 1998 (mean fledge date = 8 May ± 5.16 days, range: 2–15 May, n = 7).

DISCUSSION

The low variability between nest sites in tree species, size, cavity height, and entrance width suggests that Lilac-crowned Parrots may select nest sites based on these characteristics. Predation rates decrease with increasing height of nest sites from the ground (Nilsson 1984, Wilcove 1985), while the increased

size of nest entrance required by large birds may pose greater risks from predation, leading to specific requirements for entrance dimensions (Christman and Dhondt 1997). Amazon parrots in northeastern Mexico appear to select cavities based on tree species, cavity height, and entrance length (Enkerlin-Hoeflich 1995). Australian cockatoos also demonstrate species specific requirements related to body size for entrance dimensions and internal diameter of nest hollows (Saunders et al. 1982). Enkerlin-Hoeflich (1995) suggested that variability in several cavity characteristics combined with narrow criteria for a few key characters may provide parrots with the flexibility to exploit a wide range of available cavities while limiting predation and competition threats. In addition, low nest site reuse by Lilac-crowned Parrots is contrary to the 30–40% cavity reuse observed for most other parrot species (Saunders 1982, Snyder et al. 1987, Rowley and Chapman 1991, Smith 1991, Enkerlin-Hoeflich 1995). Natural predation is the main cause of nest failure for Lilac-crowned Parrots (Renton 1998), hence infrequent cavity reuse may help to prevent predators from learning nest site locations (Sonerud 1985, 1989).

The Lilac-crowned Parrot is notably different from other parrot species in its high synchrony in nest initiation, with all nests commencing within two weeks in each season, and the general nest initiation period comprising the first three weeks in February. There is no evidence that breeding pairs of the Lilac-crowned Parrot relay after a nest failure, which would also lengthen the nesting period. Most *Amazona* species have a 3–5 week nest initiation period each breeding season (Snyder et al. 1987, Gnam 1991, Enkerlin-Hoeflich 1995). The Monk Parakeet (*Myiopsitta monachus*) in Argentina extends egg-laying over a nine week period (Navarro et al. 1992). Australian cockatoos have a similar broad egg-laying period of 5–8 weeks (Saunders 1982, Smith and Saunders 1986, Rowley and Chapman 1991, Smith 1991). The nesting season of the Lilac-crowned Parrot may be so sharply defined by the extreme climatic seasonality in tropical deciduous forest and food resource availability. Nesting pairs may need to fledge young before the end of the long dry season in late May–June when food abundance declines (Renton 1998). Delaying nest initiation may result in breeding pairs having to conduct energetically demanding activities of raising young during this environmentally difficult period.

The infrequent feeding visits to the nest by breeding pairs of the Lilac-crowned Parrot contrasts with the multiple daily feedings noted for island *Amazona* species (Snyder et al. 1987, Gnam 1991) and other Neotropical parrots (Lanning and Shiflett 1983; Lanning 1991; Waltman and Beissinger 1992; K.R., pers. obs.), but is consistent with the two nest visits per day observed for three mainland Amazon parrots in northeastern Mexico (Enkerlin-Hoeflich 1995). Morning and afternoon arrival times, approximately one hour after sunrise and one hour before sunset, for nesting pairs of the Lilac-crowned Parrot were similar to the three *Amazona* species in northeastern Mexico (Enkerlin-Hoeflich 1995). Large cockatoos in dry areas of Australia also restrict nest visitation activity to the early morning and late afternoon, spending the hot, mid-day periods resting under the shade of leafy trees (Saunders 1982). Lilac-crowned Parrots at the study site have been noted to demonstrate signs of heat stress during the mid-day hours of 12:00–14:00 by holding wings away from their bodies and panting with beaks open (K.R., pers. obs.). Therefore, restricting feeding activity to the early morning and late afternoon may enable parrots to conserve energy during high mid-day temperatures, particularly in dry habitats.

In addition to being infrequent, nest attendance by Lilac-crowned Parrots during feeding visits was brief. Most Lilac-crowned Parrot activity was conducted away from the nest area. Nesting pairs were never observed to forage near the nest, and food transfers from the male to the female took place an average 423 m from the nest. Island Amazon parrots, by comparison, may spend longer periods in the nest cavity brooding and preening young (Snyder et al. 1987), as well as conducting food transfers and foraging activities near the nest (Snyder et al. 1987, Gnam 1991). Infrequent visits, short nest attendance, and feeding away from the nest by Lilac-crowned Parrots may serve to limit the amount of activity in the nest area, and reduce the risk of attracting predators to the nest.

Breeding birds are restricted by competing demands to maintain their own energetic requirements and to protect and nourish the young (Martin 1987). While infrequent, short nest visits may reduce both mid-day energetic expenditures by foraging adults and the risks of nest predation, there is a cost in having to meet the energy demands of the young in a shorter time. Hence, variations in nesting behavior suggest that island and mainland Amazon parrots may be employing differing strategies to meet time constraints in caring for the young.

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RELATIONSHIPS AMONG RED-COCKADED WOODPECKER GROUP DENSITY, NESTLING PROVISIONING RATES, AND HABITAT

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ABSTRACT.—We examined Red-cockaded Woodpecker (*Picoides borealis*) food provisioning rates of nestlings during the 1992 and 1993 breeding seasons on the Vernon Ranger District of the Kisatchie National Forest in Louisiana. Provisioning rates were monitored at nest trees in moderate (9.8 groups/2 km radius, $n = 10$) and low (5.9 groups/2 km radius, $n = 10$) density populations. Habitat around each cluster was measured within three radii (100 m, 400 m, and 800 m) to evaluate the possible influence of habitat quality on group density and nestling provisioning rates. We tested the null hypothesis that habitat quality and provisioning rates would be similar in areas with different densities of woodpecker groups. We failed to detect differences in nestling provisioning rates between woodpecker groups in moderate versus low group densities. Woodpecker groups from areas where group densities were moderate attempted to nest significantly more often than woodpecker groups occurring in low densities. Hardwood midstory vegetation was more abundant in areas with low woodpecker group density. Old-growth pines, which are known to be important for cavity excavation, were present in habitat around cavity-tree clusters of moderate-density groups, but generally absent in areas where group density was low. Woodpecker group density may be related to hardwood midstory conditions and the abundance and spatial distribution of remnant old pines. *Received 18 August 1998, accepted 9 August 1999.*

The Red-cockaded Woodpecker (*Picoides borealis*) is a cooperatively breeding species closely associated with older-growth pine forests of the southeastern United States (U.S. Fish and Wildlife Service 1985, Walters et al. 1988). A single tree, or aggregation of cavity trees, termed the cluster, is inhabited by a group of woodpeckers that includes a single breeding pair. Other adults present in the group are typically male offspring from previous breeding seasons (Ligon 1970, Lennartz et al. 1987).

Considerable information is known about the woodpecker's cavity tree requirements. The Red-cockaded Woodpecker requires old living pines for its cavities (Conner and O'Halloran 1987). The presence of fungal decay within the heartwood of pines increases in frequency as pines age and significantly shortens the time required for woodpeckers to excavate nest and roost cavities (Hooper et al. 1991, Conner et al. 1994, Rudolph et al. 1995). A sufficient diameter of heartwood, which increases with pine age, also is required to provide adequate space for cavity excavation (Conner et al. 1994). Pines with suitable cavities are known to be a critical resource for Red-cockaded Woodpeckers (Walters et al. 1992a, Conner and Rudolph 1995). Thus, location of existing cavities and the number and distribution of old-growth pines that can be excavated for cavities likely has a strong influence on the density and spatial distribution of woodpecker groups.

The quality of foraging habitat across the forest landscape also may influence nesting success and the density of Red-cockaded Woodpecker populations. Male and female Red-cockaded Woodpeckers forage at different locations on trees and use different methods to exploit arthropod prey (Ligon 1968, Hooper and Lennartz 1981). Hooper and Harlow (1986) observed that foraging Red-cockaded Woodpeckers showed little preference among pine stands that were more than 30 years old, and concluded that once pine stands reach 30 years old their quality as a foraging substrate does not improve with further aging. More recent studies suggest that old-growth pines provide an increased foraging benefit (Zwicker 1995, Jones and Hunt 1996, Eng-

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strom and Sanders 1997). In this study we evaluate relationships among forest habitat, adult woodpecker provisioning rates of nestlings, and woodpecker fledging success of woodpecker groups where group density is moderate and where group density is low. We ask if foraging habitat characteristics are related to woodpecker group density, nestling provisioning rates, and nesting success. If woodpecker group density is a function of foraging habitat quality, provisioning rates of nestlings where woodpecker group density is moderate might be expected to exceed those of groups living in lower densities.

STUDY AREA AND METHODS

The Vernon Ranger District of the Kisatchie National Forest (31° 01′ N, 93° 02′ W) is located in west-central Louisiana. Longleaf pines (*Pinus palustris*) compose the bulk of the overstory with grasses and forbs as the primary ground cover. Hardwood midstory vegetation is typically minimal on the Vernon Ranger District but does occur in some areas where the effectiveness of prescribed fire has been reduced. We selected 10 Red-cockaded Woodpecker groups from areas of the national forest where group density was moderate ($\bar{x}$ = 9.8 active cavity-tree clusters per 2-km radius) and 10 groups from portions of the Ranger District where group density was low [$\bar{x}$ = 5.9 active cavity-tree clusters per 2-km radius; moderate vs low group density: $t_{(18)} = 5.01$, $P < 0.001$; see Hooper and Lennartz (1995) for classification (moderate vs low) of woodpecker group densities]. Prior to the 1992 breeding season, all adult woodpeckers roosting within these 20 clusters were captured at their roost cavities, weighed, and banded with U.S. Fish and Wildlife Service metal bands and combinations of color bands to facilitate individual recognition.

At the onset of the nesting seasons during 1992 and 1993 we climbed cavity trees using Swedish climbing ladders to determine the location of the nest tree, the number of eggs in the clutch, and the initial number of nestlings. During July and August of both years we determined the number of post-fledging survivors for each woodpecker group. We quantified adult provisioning rates of nestlings for each woodpecker group when nestlings were 8, 20, and 23 days old (see Schaefer 1996). The total number of provisioning trips made by adults to feed nestlings was counted during the 3-hour period following the breeding male's initial departure from the nest cavity in the morning. We also identified which adult brought food to nestlings during each provisioning trip and made an estimate of prey size (cm) using the adult woodpecker's bill as a size scale. Nest trees were climbed after each 3-h provisioning sampling period to verify the number of nestlings present in each nest cavity. An adjusted provisioning rate was calculated for each nest by dividing the total number of feeding trips by the number of adult woodpeckers in the group, yielding the number of provisioning trips per adult. Provisioning rates were also adjusted to simultaneously account for different numbers of nestlings in cavities and group size.

Red-cockaded Woodpecker use of forest stands for foraging depends in part on the distance of the stand from cavity trees (DeLotelle et al. 1987). We measured vegetational characteristics around the geometric center of each woodpecker cavity-tree cluster within three radii: 0–100 m, 101–400 m, and 401–800 m. Forest compartment stand maps were obtained from the Kisatchie National Forest supervisor's office for those compartments falling within 800 m of each cluster studied. Each compartment is comprised of forest stands of varying size and tree age. Five dominant or codominant pine trees were randomly selected as central points in each forest stand, and habitat characteristics for each stand were gathered around each of these five trees. For each stand, means were calculated for each habitat measurement taken around the five central trees.

Stand age was determined by coring each central tree at breast height (1.3 m) with an increment borer and counting the growth rings of the cores. Five years were added to the growth ring counts for longleaf pine to adjust for the minimum years spent as a seedling (Conner and O'Halloran 1987). Stands were divided into five age classes: 0–29, 30–49, 50–69, 70–89, and >90 years old. The diameters of each central tree and of all live stems larger than 2 cm within 11.3 m of the central tree were measured at breast height with calipers. Stands were divided into two diameter classes based on average diameters of pines: 30–40 cm and 40.1–50 cm diameter at breast height (dbh). Pines in smaller diameter classes were excluded because they were rarely encountered. A one-factor metric basal area prism was used to measure pine overstory basal area (m^2/ha). Stands were divided into three basal area classes based on average basal areas of overstory pines: 0–3, 3.1–12, and 12.1–21 m^2/ha.

Hardwood midstory density was visually estimated and placed into one of five categories: none, sparse, moderate, dense, and very dense. The effects of midstory height (measured with a clinometer) and midstory density may not be obvious when considered independently. For example, tall, dense midstory conditions may have a different impact on the woodpeckers than would tall, sparse midstory conditions. Therefore, both midstory height and midstory density were considered together to obtain measures of suitable and unsuitable midstory conditions. Midstory conditions were considered suitable if the height was less than 3 m regardless of the density, or if the density was none to sparse regardless of the height. Midstory conditions were considered unsuitable if the height was more than 3 m and the density was moderate to very dense.

The area (ha) of each forest stand within distance zones of 100 m, 400 m, and 800 m from each nest tree was measured with a digitizer using Sigma-Scan®. The area of each stand was summed for each habitat vari-

TABLE 1. Comparisons of mean (± SD) nestling provisioning (feeding) and nest productivity rates between Red-cockaded Woodpecker groups in areas of moderate (n = 10) and low (n = 10) woodpecker group density on the Vernon Ranger District, Kisatchie National Forest, Louisiana, during the 1992 and 1993 breeding seasons.

Variable	Group density		t	P
	Moderate	Low		
No. feeding trips to 8-day-old nestlings	37.0 (17.3)	37.6 (15.5)	0.61	>0.05
No. feeding trips to 20-day-old nestlings	42.1 (17.5)	43.9 (29.2)	0.19	>0.05
No. feeding trips to 23-day-old nestlings	42.6 (18.4)	46.1 (19.6)	0.06	>0.05
Adjusted 8-day feeding rate	12.9 (7.4)	13.3 (4.0)	0.13	>0.05
Adjusted 20-day feeding rate	14.3 (5.9)	15.5 (9.5)	0.38	>0.05
Adjusted 23-day feeding rate	14.8 (6.3)	16.2 (5.1)	0.57	>0.05
No. adult woodpeckers in group	3.1 (0.9)	2.9 (0.8)	0.48	>0.05
No. of eggs in clutch from successful groups	3.1 (0.9)	2.8 (1.2)	0.80	>0.05
No. of nestlings fledged from successful groups	1.9 (0.9)	1.7 (0.9)	0.67	>0.05

able by age, dbh, and basal area classes as described above for the 100 m, 400 m, and 800 m concentric distance zones around each woodpecker cluster examined and converted to a percentage for each distance zone.

Data were analyzed using SAS (version 6.12; SAS Inst. Inc. 1988) on an IBM compatible computer. Percentage data for stand area in various habitat classes were transformed with an arcsin transformation, and count data for nesting variables were transformed with a square root function to approximate normality in all parametric statistical tests. A stepwise discriminant analysis was used as a data reduction technique to compare habitat variables between groups occurring in moderate and low densities. In order to test the hypothesis that habitat quality influences provisioning rates and woodpecker group density, we calculated two-tailed t-tests (adjusted for unequal variances) to test for differences in nest productivity and provisioning effort. Frequencies of nest success, nest attempts, and nest failures for moderate and low group densities were compared with χ^2 analysis using 2 × 2 contingency tables. Logistic regression (stepwise) was used to evaluate nest success (successful or not) and nest attempts (attempted to nest or not) as a function of habitat characteristics.

RESULTS

Of all habitat variables measured only the percentage area with suitable midstory conditions within 100 m of the nest tree (Wilks' Lambda 0.78, P = 0.0356, 1, 18 df) entered the stepwise discriminant function (75% classification accuracy) comparing groups in moderate [96.3% ± 6.5 (SE) area with suitable midstory] and low (67.8% ± 38.5) densities, suggesting considerable homogeneity of habitat throughout the Vernon Ranger District. Stands with old-growth pines (pines >90 years old) within 100 m and 400 m of clusters were present around groups occurring in moderate densities (1.7% ± 5.2 and 2.4% ± 5.7 of the area, respectively) but were totally absent in areas with low woodpecker group densities.

Differences in woodpecker group density did not appear to be a function of foraging habitat quality. We detected no significant differences between moderate and low woodpecker group density in the unadjusted and adjusted rates that adults fed nestlings at 8, 20, or 23 days post hatching, woodpecker group size, clutch size, and the number of young successfully fledged (Table 1). However, the power of our ability to detect a difference is low (5–9%) because of the relatively small sample size (n = 20). As with provisioning rates, we failed to detect a difference between moderate and low woodpecker group density in the size of prey that adults fed to nestlings (t = 0.45, $P > 0.05$, df = 24). The average weight of breeding males was identical in areas of moderate group density (48.3 g) and low group density (48.3 g). Breeding female woodpeckers differed by only 0.1 g, 46.6 g and 46.7 g, respectively.

A significantly higher proportion of woodpecker groups attempted to nest in moderate group densities (19 of 20 nest years) than in low group densities (10 of 20 nest years; χ^2 = 10.2, $P < 0.001$, df = 1). Also, a significantly higher proportion of woodpecker groups nested successfully in moderate group densities (17 of 20 nest years) than in low group densities (9 of 20 nest years; χ^2 = 7.03, P = 0.008, df = 1). The three groups that failed to produce fledglings in the areas with moderate group density were the result of two

nesting attempts that failed and one instance where the woodpeckers did not attempt to nest because the breeding female abandoned the cluster (or died) immediately prior to the breeding season. The 11 groups that failed to produce fledglings in the low-density groups were the result of one attempt (eggs laid) that failed, five instances where the breeding female disappeared immediately prior to the breeding season, and five instances where a pair was present but did not attempt to nest. Two (10.5%) of 19 nesting attempts in areas with moderate group density failed, whereas 1 (10.0%) of 10 nesting attempts in areas with low group density failed ($\chi^2 = 0.002$, $P > 0.05$, df = 1). Cluster abandonment by females prior to the breeding season was marginally higher in low group densities (5 of 20 nest years) than in moderate group densities (1 of 20 nest years; $\chi^2 = 3.14$, $P = 0.08$, df = 1).

Attempts to evaluate nest success (successful or not) and nest attempts (attempted to nest or not) as a function of habitat characteristics through logistic regression failed as no measured habitat characteristic had a sufficient relationship to enter the analyses.

DISCUSSION

The observed lower rate of nesting attempts in the low-density groups relative to moderate-density groups could be related to at least several factors singly or in combination: (1) failure to nest because of a foraging habitat insufficiency, (2) demographic dysfunction resulting from increased isolation of low-density groups relative to moderate-density groups, and (3) an inadequate number of older-growth pines suitable for nest trees. Inadequacy of foraging habitat appears to be an unlikely explanation. The lack of older-growth pines in the low group density area may have reduced the number of sites available for cavity-tree clusters, and because of increased group isolation, may have had a negative effect on population demographics. Unfortunately, the historic demographics of groups we studied was not known. It is also possible that prey availability, as provided by these older-growth pines, had an influence on cluster abandonment by females and whether groups attempted to nest or not. Limiting factors appear to prevent nest initiation rather than decreasing the success rate of nesting attempts.

Recent research suggests that Red-cockaded Woodpeckers have a preference for older pines. Zwicker (1995), Engstrom and Sanders (1997), and Jones and Hunt (1996) observed that Red-cockaded Woodpeckers used larger, older-growth pines at much higher rates than would be expected based on availability. However, using logistic regression we failed to detect a relationship between availability of old pines and nesting attempts.

The age and experience of the breeders occupying moderate and low density group areas also may have influenced the observed differences in nesting productivity. Older and more experienced woodpeckers might preferentially capture and occupy habitat with higher densities of older-growth pines because such habitat is viewed as better quality than habitat lacking older-growth pines. The number of young fledged by Red-cockaded Woodpeckers is known to increase with the age and experience of breeders (Walters et al. 1992b). We did not know the ages of the woodpeckers in the groups we studied.

The suitability of hardwood midstory conditions within 100 m of the center of cavity-tree clusters was significantly greater for moderate-density groups, but it was not related to nest productivity or the propensity of groups to nest. The greater presence of unsuitable midstory conditions in areas of low group density than areas of moderate group density suggests that cluster abandonment could also have influenced the observed differences in group density. The Red-cockaded Woodpecker's requirement for open pine stands relatively devoid of hardwood midstory is well known (Conner and Rudolph 1989, Loeb et al. 1992).

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RESPONSES OF BELL'S VIREOS TO BROOD PARASITISM BY THE BROWN-HEADED COWBIRD IN KANSAS

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ABSTRACT.—I studied patterns of cowbird parasitism and responses to this parasitism by Bell's Vireos (*Vireo bellii*) in Kansas. Bell's Vireos abandoned parasitized nests at a significantly higher rate than unparasitized nests. Lower probability of brood parasitism later in the season may help make abandonment followed by renesting beneficial. Burial of cowbird eggs by vireos was also observed in several cases. I did not detect a strong relationship between nest site vegetation characteristics and the probability of brood parasitism. *Received 9 Nov. 1998, accepted 27 May 1999.*

Bell's Vireo (*Vireo bellii*) is a well known host of the brood parasitic Brown-headed Cowbird (*Molothrus ater*; Barlow 1962, Mayfield 1965, Franzreb 1987, Brown 1993). The arrival of the cowbird in California in this century (Laymon 1987) has been cited as a major factor causing the severe range restriction and endangerment of the Least Bell's Vireo (*V. b. pusillus*; Franzreb 1987, 1989; Laymon 1987, Brown 1993). In his review Brown (1993) reported that between one third to over one half of all Bell's Vireo nests monitored in California were parasitized by cowbirds. High rates of parasitism were also reported in the Great Plains race (*V. b. bellii*; Barlow 1962, Brown 1993). Although declines in Bell's Vireo population have been detected in some areas of the Great Plains by the Breeding Bird Survey (Brown 1993), this species is still at least locally common. The long-term data set (1981–1997) from my study site shows no decline [Konza Prairie Long Term Ecological Research (LTER) Site, data set CBP01]. Surveys elsewhere in the region also have detected higher Bell's Vireo densities than nearby Breeding Bird Survey routes (Robbins et al. 1992, 1993; M. B. Robbins, pers. comm.). This suggests that cowbird parasitism, despite its frequency, may not be causing a rapid decline in Bell's Vireo on the Great Plains.

It is important to study nest success because local population numbers may not reflect local reproduction (because of source-sink dynamics; Brawn and Robinson 1996). If the Bell's Vireo is not declining rapidly on the Great Plains, we might expect this population to possess traits that would allow its persistence in the face of cowbird parasitism. Vireos could try to avoid parasitism altogether, they could attempt to salvage nesting attempts after parasitism has occurred, or they could simply abandon parasitized nests and renest (Clark and Robertson 1981, Hill and Sealy 1994). Avoidance measures could include cryptic nest placement, secretive behavior around the nest (Uyehara and Narins 1995), and/or aggressive nest defense (Neudorf and Sealy 1994, Robertson and Norman 1977). Two means of salvaging a parasitized nest include removal of cowbird eggs (Rothstein 1975) or burial of cowbird eggs with nesting material (Clark and Robertson 1981, Sealy 1996).

In this paper, I consider the potential roles for avoidance of cowbirds and salvaging or abandoning parasitized nests by Bell's Vireos in Kansas. Analysis of nest site vegetation coupled with observations of nest contents allowed exploration of cryptic nest placement, burial of cowbird eggs, and nest abandonment followed by renesting.

METHODS

From May through August of 1996 I investigated cowbird parasitism and nest success of Bell's Vireos in the Flint Hills of northeastern Kansas. My study site was located on a portion of the Nature Conservancy's Konza Prairie Research Natural Area (in Riley and Geary counties). The site consisted of tallgrass prairie interspersed with deciduous shrub vegetation concentrated around ephemeral streams and limestone outcroppings. Vireos arrive at this site beginning in mid-May and initiate nest building in late May, but renesting attempts continue into early July. Nests are

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placed in low deciduous shrubs usually within 1.5 m of the ground (unpubl. data).

Nest building by Bell's Vireos usually takes 3 to 4 days and egg laying follows 1 or 2 days after nest completion. Males aid in nest site selection, nest construction, incubation, and feeding of young. Typically 4 eggs are laid (Brown 1993). On the Great Plains, two broods are sometimes reared in one season (Barlow 1962, Brown 1993).

I searched for and monitored nests throughout the season using the locations of singing males to narrow my search. I located most nests before the onset of incubation. The entire study area (110 ha) was searched every 3–4 days. I also visited active nests once every 3–4 days to record the number of eggs and/or nestlings present (including cowbird) and to look for any buried cowbird eggs. If no adult vireo was active in the vicinity of the nest, I felt the eggs for warmth to determine if they were being incubated. I ceased visiting a nest and concluded it had failed after two successive visits where I observed cold eggs and no parental activity. If the entire contents of a nest were removed, or if during incubation or the nestling period most of the contents were removed and the parents ceased attending the nest, I concluded that the nest was depredated. I did not visit nests if cowbirds or predators were in the vicinity (Martin and Geupel 1993).

To minimize nest disturbance, I waited until the nest was no longer in use before assessing vegetation near the nest. I measured height of nest, height of the nest shrub, and depth of leaf litter. I counted the number of woody stems within a 50 cm horizontal radius of the nest shrub and estimated nest concealment (percentage of nest hidden from the observer by vegetation at distance of 1 m, BBIRD protocol) above, below, and in the four cardinal directions around the nest. I estimated ground cover (a proxy for vegetation density; defined as the percent of ground covered by a given vegetation type within 5 m of the nest) for nest substrate (the plant species in which nest placed), large shrubs (the size class used by vireos for nesting), all woody vegetation, woody clumps (closed canopy continuous woody vegetation), sparse woody clumps (open canopy continuous woody vegetation), grass, and the three most common woody species within 5 m. Also within the 5 m, I estimated the median height of the woody canopy, measured the height of the tallest woody stem, and counted the number of dead woody stems and the numbers of live woody stems under 2.5 cm diameter and over 2.5 cm diameter. To assess the area of ground covered (both within and outside of the 5 m radius) by the woody clump in which the nest was placed, I measured the maximum width of the clump and the width perpendicular to the maximum. The distance from the nest to the nearest corridor of woody vegetation along a stream bed was recorded as well.

By noting changes in nest contents and whether or not nests were active, I assessed vireo responses to cowbird parasitism: nest material placed over cowbird eggs or nest abandonment subsequent to the laying of cowbird eggs. A nest was considered abandoned (as opposed to depredated) if parental activity ceased and either the number of vireo eggs had not declined between visits or the number of vireo eggs had decreased but the number of cowbird eggs had increased between visits. Using a χ^2 test (Sokal and Rohlf 1987), I compared the proportion of parasitized nests that were abandoned to the proportion of unparasitized nests which were abandoned. All completed (nest lining complete), active (adults defending nest) nests located before or during the laying stage were included in the analysis ($n = 63$).

TABLE 1. Fates of Bell's Vireo nests parasitized and not parasitized by Brown-headed Cowbirds. All nests included were completed and active and were found during building or laying.

	Parasitized nests	Unparasitized nests
Abandoned	32[a]	8[b]
Depredated	8[b]	4
Fledged (cowbird if parasitized, vireos if not)	3	8[c]
Total[d]	44	19

[a] Includes two nests in which cowbird eggs were buried and other cowbird eggs were later laid.
[b] Includes one nest in which a cowbird egg was buried.
[c] Total offspring fledged = 24.
[d] One nest counted as parasitized here contained a buried cowbird egg. Without further cowbird eggs being laid, the nest was later abandoned and so was considered unparasitized when abandoned.

To identify the factors associated with nest abandonment, I compared parasitized nests ($n = 43$; does not include 1 nest abandoned after vireos had buried a cowbird egg; Table 1) that were abandoned to those that were not abandoned based on the numbers of vireo eggs and cowbird eggs in the nests. Numbers of vireo and cowbird eggs were considered separately in two *t*-tests (using *t*-test assuming equal variances, Microsoft Excel 7.0).

Although the vireos were not banded, I conservatively estimated renesting attempts by comparing nest locations with dates of nest use for all nests ($n = 63$) included in this study. I considered a nesting attempt to be a renesting event if it occurred within 7 days of the cessation of use of a nearby nest. If a nesting attempt was begun after a longer period, I considered it a possible renesting attempt (presumably in some of these cases I may have missed an intervening nesting attempt). Furthermore, a nest could be considered part of a given series of renestings (or possible renestings) only if the location of the nest did not overlap with the locations of a different series of apparent renestings. Because Bell's Vireos are territorial (Brown 1993), I made the conservative assumption that territories (i.e., series of nesting attempts) did not overlap and were consistent throughout the season to avoid overestimating renesting. I located a number of isolated nests which, based on their late dates of initiation,

were probably renesting attempts; however, I did not count these as renestings because I could not identify any previous nests.

A reasonable estimate of the proportion of pairs producing offspring was not possible because for 25 of the estimated 33 vireo pairs, only one or two nesting attempts were observed for each pair. Therefore I could not rule out the possibility that other, possibly successful, nesting attempts were not detected.

To assess the timing of nest initiation on nest success, I conducted the following analyses. I compared vireo nest initiation dates (Julian dates) for both parasitized and unparasitized nests ($n = 56$) using a Mann-Whitney *U*-test. This analysis included all completed, active nests found during building or laying except for those unparasitized nests that were abandoned early in the nesting cycle ($n = 7$). For the nests I excluded from the analyses, I could not rule out the possibility that parasitism might have occurred had the nest remained in use. I also compared the nest initiation dates for both depredated and fledged (fledged either cowbird or vireo young) nests ($n = 23$) using a Mann-Whitney *U*-test. Included in this analysis were completed, active nests found during building or laying that were either depredated or fledged. Finally, using a Mann-Whitney *U*-test, I compared vireo nest initiation dates for successful (fledged vireos) and unsuccessful (all other fates) nests. All 63 complete, active nests found during building or laying were included. *U*-test *P*-values were obtained from Sokal and Rohlf (1987).

I included 28 variables describing vegetation surrounding nests in a step-wise discriminant function analysis (using PROC STEPDISC, SAS 6.12, for a UNIX operating system) to compare parasitized to unparasitized nests. I set the critical *P*-value for entering and remaining in the model at 0.05. I included nests found at all stages of the nesting cycle for which I had measured vegetation (unparasitized $n = 15$, parasitized $n = 50$) except for those unparasitized nests that were abandoned early in the nesting cycle. For these abandoned nests, I could not rule out the possibility that parasitism might have occurred had the nest remained in use.

RESULTS

Of the 63 completed and active Bell's Vireo nests found during nest building and laying, 44 (70%) were parasitized by at least one cowbird egg but only 3 of these fledged a cowbird young (Table 1). None of the parasitized nests fledged any vireo young. A mean of 1.5 cowbird eggs were laid in each parasitized nest, and a mean of 1.5 vireo eggs were present in each such nest after cowbird activity (possibly egg removal; Brown 1993).

Of the 44 parasitized Bell's Vireo nests included in this analysis, in only 4 (9%) did the vireo parents use additional nest material to cover one or more cowbird eggs laid in their nests. All nests with buried eggs subsequently failed for a variety of reasons (Table 1). In none of the nests with buried eggs could I rule out the possibility that cowbird eggs had been buried during the process of nest building because they were laid in nests under construction.

Nest abandonment following cowbird parasitism in my study was frequent. Of the 43 parasitized nests (does not include 1 nest abandoned after vireos had buried cowbird egg, see Table 1), 32 were abandoned. This is a significantly higher proportion of abandonment than that expected based on the frequency of abandonment for unparasitized nests (8 of 20; $\chi^2 = 21.22$, $P < 0.001$).

Abandoned nests had significantly fewer host eggs than non-abandoned nests [abandoned: $\bar{x} = 0.9 \pm 0.1$ (SE); non-abandoned: $\bar{x} = 3.3 \pm 0.1$; $t = -7.04$, $P < 0.001$]. Abandonment was not significantly related to the number of cowbird eggs laid (abandoned: $\bar{x} = 1.6 \pm 0.1$; non-abandoned: $\bar{x} = 1.2 \pm 0.1$; $t = 1.45$, $P > 0.05$).

Of 63 nests, I estimated 20 (32%) were renesting attempts and 10 (16%) were probable renesting attempts. Of the 8 nests that fledged vireo young, 6 appeared to have been renesting attempts.

Unparasitized nests ($n = 12$) were initiated significantly later ($U = 378$, $P < 0.05$) than parasitized nests ($n = 44$; Fig. 1). No difference in initiation date was found between depredated ($n = 12$) and fledged ($n = 11$) nests in initiation date ($U = 91$, $P > 0.05$; Fig. 1). Successful nests ($n = 8$) did not differ from failed nests ($n = 55$) in date of initiation ($U = 235.5$, $P > 0.5$; Fig. 1).

The nest substrate species was selected by step-wise discriminant analysis as a significant predictor of cowbird parasitism ($F = 5.29$, $P = 0.0248$, $r^2 = 0.08$). Unparasitized nests were surrounded within 5 m by more of the plant species in which the nest was placed than were parasitized nests. No other vegetation variables distinguished parasitized from unparasitized nests.

DISCUSSION

During my one season of study, abandonment (and apparent renesting) was the most common response of Bell's Vireos to brood

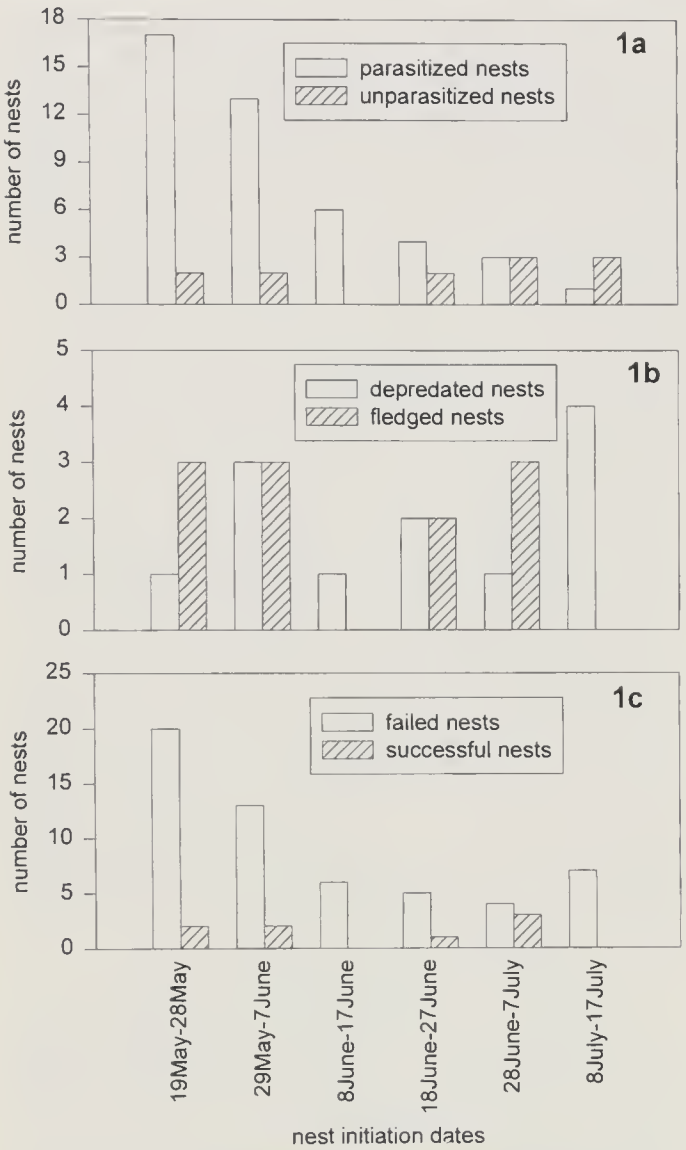

FIG. 1. Dates of Bell's Vireo nest initiation (in 10 day intervals; May–July 1996) for (1A) parasitized and unparasitized nests, (1B) depredated and fledged (either cowbird or vireo young) nests, and (1C) failed and successful (Bell's Vireo fledged) nests.

parasitism by cowbirds. Abandoned nests had fewer host eggs than non-abandoned nests. This result is consistent with other findings that egg removal by cowbirds, rather than the presence of cowbird eggs in the nest, is the stimulus that leads to nest abandonment (Barlow 1962, Hill and Sealy 1994, Woodworth 1997). It is also consistent with the hypothesis that nest abandonment is a generalized response to egg loss as opposed to a specific response to parasitism (Rothstein 1975).

The seasonal activity of Brown-headed Cowbirds could be a factor favoring nest abandonment by the Bell's Vireo. Unparasitized vireo nests were initiated significantly later in the season. Egg laying by cowbirds declined more quickly than vireo nest initiation over the breeding season at my study site; a finding similar to other studies (Scott and Ankney 1980, Hill and Sealy 1994). Those Bell's Vireos that nest later therefore are less likely to be parasitized. This suggests that nest abandonment followed by renesting is beneficial for the vireos. No costs to later nesting were detected; neither depredated nests nor nests that failed from all causes differed in initiation date from successful nests. However, post-fledging success was not followed.

Nest abandonment may be a complementary tactic to egg burial. Abandonment may be effective at high rates of parasitism while egg burying may be effective at lower rates. In this study, burying of cowbird eggs was rare and was not a successful tactic, partially because of subsequent cowbird parasitism. However, when rates of parasitism are lower (i.e., with a lower probability of subsequent cowbird eggs being laid) this behavior might be beneficial. Burial is probably less expensive energetically than constructing a new nest (Clark and Robertson 1981). Frequency of parasitism on my study site may be unusually high in comparison to the Great Plains as a whole (29% of nests parasitized, Friedmann et al. 1977; 13–69% of nests parasitized, Brown 1993). If this is so, then this study may underestimate the importance of egg burying in allowing Great Plains Bell's Vireos to persist in the presence of cowbirds.

Egg burying has not been reported for Bell's Vireos in California (Salata 1983, Gray and Greaves 1984, Franzreb 1989). Cowbirds have occupied most of California only in the past century (Laymon 1987), so their hosts there may not have had enough time to evolve adaptive responses to brood parasitism (Mayfield 1965).

I did not attempt to compare cowbird induced nest abandonment rates in my study to those reported from California because of two potentially confounding factors. Unlike my study, in California cowbird eggs were removed by researchers (Salata 1983, Gray and Greaves 1984, Franzreb 1989). Therefore, the observed rate of abandonment in California may be reduced because not all vireos that abandon parasitized nests do so immediately upon receiving a cowbird egg (pers. obs.). Secondly, usually only one cowbird egg was

laid per nest in California (Salata 1983, Gray and Greaves 1984, Franzreb 1989), possibly coinciding with removal of only one host egg by the cowbirds (Lowther 1993). The lower intensity of parasitism in California than in Kansas could mean a less intense proximate cue for vireos to abandon in California. This could lead to the observation of different abandonment tendencies in these two vireo populations regardless of the presence or absence of any evolved differences between them.

To better understand cowbird behavior and the possibility for cryptic nest placement by vireos, I considered the relationship between nest-site vegetation and parasitism. I found that unparasitized nests had more ground covered (within 5 m of the nest) by the plant species in which a given nest was placed (nest substrate). However, this finding does not necessarily support the idea that an increased density of vegetation generally hinders searching by cowbirds because no other measures of vegetation density were associated with brood parasitism. Although cowbird parasitism seems to be affected by vegetation structure in forests (Brittingham and Temple 1996), such effects were not apparent in this study. The predictive value of the variable 'nest substrate' was low ($r^2 = 0.08$). With such a weak relationship between nest placement and brood parasitism, cowbirds may be a negligible selective pressure further refining nest placement in the Bell's Vireo.

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THE TYPE B SONG OF THE NORTHERN PARULA: STRUCTURE AND GEOGRAPHIC VARIATION ALONG PROPOSED SUB-SPECIES BOUNDARIES

MICHAEL D. BAY[1,2]

ABSTRACT.—The type B song of the Northern Parula (*Parula americana*) was described from 120 males recorded throughout much of the species' range in North America. Most songs were structured with a series of complex syllables, followed by simple syllables, trill syllables, and a terminal simple syllable. Some birds sang songs that contained 2 phrases per song with syllables that varied in structure and number between individuals. Analysis of song variables revealed variation at the macrogeographic level with songs from western populations differing significantly from eastern populations in song duration, frequency, number of trill syllables, and simple syllables. In addition, variation was evident between eastern and western populations in the structuring of phrase patterns. *Received 8 March 1999, accepted 3 August 1999.*

Several investigations into wood-warbler (Parulidae) song behavior have shown that some species sing two song types (Ficken and Ficken 1967, Morse 1967, Highsmith 1989) while other species have a repertoire of several songs classified as first and second category songs (Lein 1978, Staicer 1989, Byers 1995). The two song types have been referred to as types A and B (Morse 1967, Nolan 1978), types I and II (Lanyon and Gill 1964, Gill and Murray 1972, Morrisson and Hardy 1983), or accented and unaccented ending songs (Morse 1966, Lein 1978). Studies on the function of song suggest that type A, I, or accented ending songs [or the type B in Black-throated Green Warblers (*Dendroica virens*) and Blackburnian Warblers (*D. fusca*)] are used as intersexual signals and are more stereotyped; while B, II, or unaccented ending songs (or the type A in Black-throated Green and Blackburnian warblers) are used intrasexually and tend to be more variable (e.g., Kroodsma 1981, reviewed by Spector 1992).

Although detailed descriptions of parulid song types can be found for several species, a few, like the Northern Parula (*Parula americana*), are less well studied. Moldenhauer (1992) presented a detailed account of the type A song, but the type B song has yet to be described in detail spectrographically. In this study, I present a description of B songs recorded from several males located throughout the species' breeding range (eastern United States and southeastern Canada).

METHODS

Type B songs of 29 male Parula Warblers were recorded from 20 localities in Texas, Alabama, Mississippi, Louisiana, Georgia, and Tennessee (Appendix) from 15 May to 10 June 1986, during the morning hours of 07:00–10:00 (CST). Although no birds were color marked, only 1–3 individuals were recorded per locality, with two investigators recording different individuals, often at the same time. Type B songs were, in most instances, elicited by song playback. These recordings (46 songs) were made using a Uher 4000 Report IC recorder at a tape speed of 19 cm/sec and a Dan Gibson P650 parabolic microphone. Spectrograms of recorded songs were produced with a Kay Elemetrics 6061B sonagraph with a wideband filter. Additional song recordings were obtained from the Texas Bird Sound Library (Department of Biological Sciences, Sam Houston State University; 33 birds, 50 songs), Cornell Library of Natural Sounds (15 birds, 27 songs), and the Borror Laboratory of Bioacoustics of The Ohio State University (43 birds, 58 songs). These songs were recorded using Nagra III (38 cm/sec) or Magnemite (38 cm/sec) recorders. An AKG microphone (or an unknown type) was used with a parabola to record.

The following variables were measured for each song: (1) duration of song (sec), (2) total number of syllables, (3) number of syllable types, (4) minimum frequency, and (5) maximum frequency. For individuals with multiple recordings, I computed a within-bird mean. For the sake of comparison with variation as reported in the type A song (Moldenhauer 1992), I used analysis of variance (ANOVA; SAS Institute 1985; $\alpha = 0.05$) to test for significant differences between song populations from three geographic areas. Moldenhauer (1992) primarily reported on the differences between songs in the western versus eastern regions of the species' breeding range. I followed this

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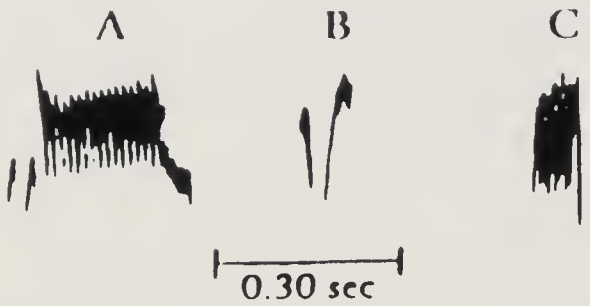

FIG. 1. Syllable classes of Northern Parula type B songs. (A) complex syllable (B) simple syllable (C) trill syllable.

division with the exception that I divide the eastern population into northeast and southeast (see Appendix). These geographical ranges correspond to the subspecies (western race, *P. a. ludoviciana*; southeastern race, *P. a. americana*; northeastern race, *P. a. pusilla*) proposed by Oberholser (1974).

I classified song elements based on morphological structure (Baptista 1974, Weins 1982, Bradley and Bradley 1983) using terminology partly adopted from Baptista (1974) and Staicer (1989). A note was any short tracing on the spectrogram, and syllables were represented by repeated notes or series of notes forming a coherent unit. Three classes of syllables were identified: (1) simple syllables (SS), those containing 1 or 2 simple notes; (2) complex syllables (CS), syllables with more than 2 notes forming a coherent unit, or in rare instances 1–2 wavy and continuous notes; (3) trill syllables (TS), high frequency slurs near the end of a song (Fig. 1). To distinguish between the number of different variations or types within each syllable class, a subscript number was added to a syllable's abbreviation (e.g., CS_{14}).

A phrase was defined as a series of repeated syllables forming the following 4 phrase classes of a B song: (1) complex (C) phrase, composed of complex syllables of one type; (2) mixed (M) phrase, composed of a mixture of repeated complex and simple syllables of one type each; (3) trill (T) phrase, composed of trill syllables of one type; (4) repeated trill (R) phrase, composed of trill syllables of 2 types (Fig. 2). A phrase pattern was the entire sequence of phrases in a song and was symbolized by the letter codes for each phrase class (e.g., C-T-SS = a song composed of a C phrase, T phrase, and ending with a simple syllable; Fig. 3).

RESULTS

Song structure.—Thirty-nine syllable types from 3 syllable classes were discovered in the type B song, including 21 complex syllables (Fig. 4), 11 simple syllables, and 7 trill syllables (Fig. 5). It appeared that no one individual contained more than one complex syllable type and no more than 2 types of simple and trill syllables.

Each of the syllable classes (complex, simple, and trill) was used to construct song phrases that typically began with an introductory series of complex syllables ($\bar{x}$ = 3.6 syllables per song, SD = 1.4, n = 181 songs) followed by a high frequency trill (T phrase) ($\bar{x}$ = 4.6 syllables per song, SD = 2.7, n = 181 songs) and ending in one to several simple syllables (SS; $\bar{x}$ = 0.88 syllables per song, SD = 2.6, n = 181 songs). Some birds sang songs that lacked a few of these syllable classes (e.g., only the introductory complex syllables were present) and therefore were shorter and usually more difficult to hear (low amplitude; e.g., somewhat like muted songs; Morse 1967). The number of syllables within a song ranged from 2 to 19.5 ($\bar{x}$ = 10.7), while most (54%) were composed of 10 to 15 syllables. Few songs contained more than 15 syllables (12.6%). Some birds began their song with chip notes (see Morse 1967) but this was rarely recorded and was not considered in this analysis.

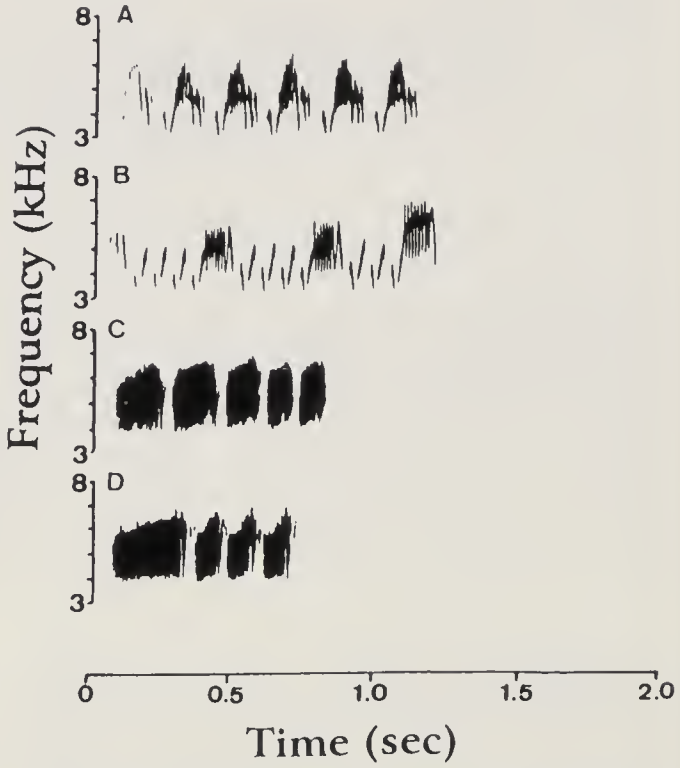

FIG. 2. Phrase classes of Northern Parula type B songs. (A) C phrase (B) M phrase (C) T phrase (D) R phrase.

The most frequent phrase pattern, C-T-SS (complex-trill-simple syllable), accounted for most of the songs (67%). Nine different patterns were found, the five most common are illustrated in Fig. 6. It is likely that some extremely rare patterns may represent scrambled

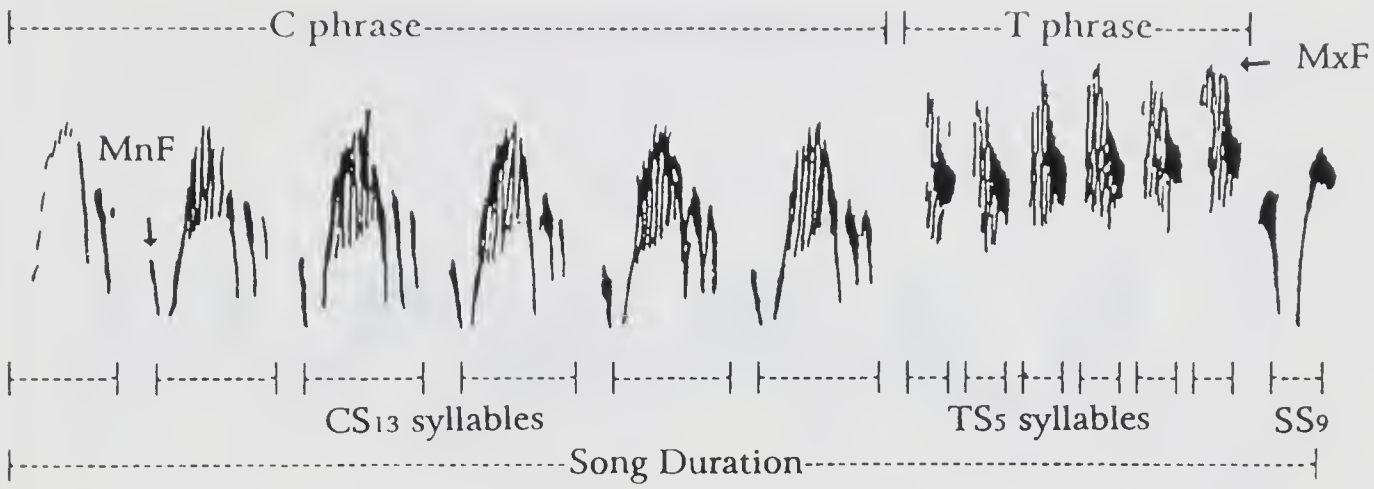

FIG. 3. Measurements and coding of a type B song. MxF = maximum frequency, MnF = minimum frequency, CS = complex syllable, TS = trill syllable, SS = simple syllable.

(e.g., T-M-T-SS occurred in 0.4% of songs) or incomplete song phrases (e.g., M occurred in 1.4% of songs and M-T occurred in 1.5% of songs).

Geographic variation.—Eight phrase patterns (except for the phrase C-T-SS) occurred in populations that occupied the western half of the species' breeding range and correspond to those birds that sang the western type A song (see Moldenhauer 1992). Birds occupying the eastern range and corresponding to those that sing the eastern type A song, sang B songs that were constructed of only three phrase patterns (C-T-SS, C-T, C; Fig. 6). The additional variation in phrase patterns observed for the western population is attributed to the addition of simple and complex syllables to the introductory portion of the song to form M phrases. This phrase difference appears to change or overlap between the Mississippi and Alabama boundary much as occurs with the type A song (Moldenhauer 1992). However, more data are needed to determine the distribution of type B song phrase patterns within the east to west type A song overlap zone.

In addition to phrase variation, songs varied significantly between geographic areas in mean duration, mean maximum frequency, and in the mean number of simple and trill syllables (Table 1). Songs of western birds averaged 0.10 second longer than songs of southeastern birds and 0.20 second longer than songs of northeastern birds ($F = 10.90$, df = 2, 134, $P < 0.001$). Birds from the latter region averaged 0.5 kHz less than the average maximum frequency of western and southeastern populations ($F = 4.31$, df = 2, 134, $P < 0.025$).

Comparing the usage of syllable types within the 3 syllable classes (complex, simple, and trill) among birds in the three geographic areas, the most frequent syllable for western birds was CS_{13} (56.6%; Fig. 4, no. 13) followed by T_2 (43.9%; Fig. 5, no. 8) and SS_8 (29.2%; Fig. 5, no. 8). For birds in the southeast, songs most frequently contained SS_8 (47.3%; Fig. 5, no. 8) followed by T_1 and T_2 (both at 39.4%; Fig. 5, no. 1 and 2, respectively). The most frequently used complex syllables for southeastern songs were CS_{13} (18.4%; Fig. 4, no. 13) and CS_4 (15.7%; Fig. 4, no. 4). Birds from the northeastern region primarily used T_3 (51.2%; Fig. 5, no. 3), CS_{19} (36.5%; Fig. 4, no. 19), and SS_9 (34.1%; Fig. 5, no. 9) to construct their songs. Of the three syllable types used to construct the type B song, significant differences were evident between the three geographical areas in the mean number of syllables used per song (Table 1). For instance, western singers used significantly more simple syllables to construct the type B song ($F = 16.3$, df = 2, 134, $P < 0.005$) but fewer trill syllables in comparison to eastern singers ($F = 23.9$, df = 2, 134, $P < 0.005$).

Only within specific localities did some birds sing identical songs (i.e., same phrase patterns and/or syllables), while others sang songs using a different type of one or more syllables within the three syllable classes (e.g., one individual might use CS_{13} and T_6, while

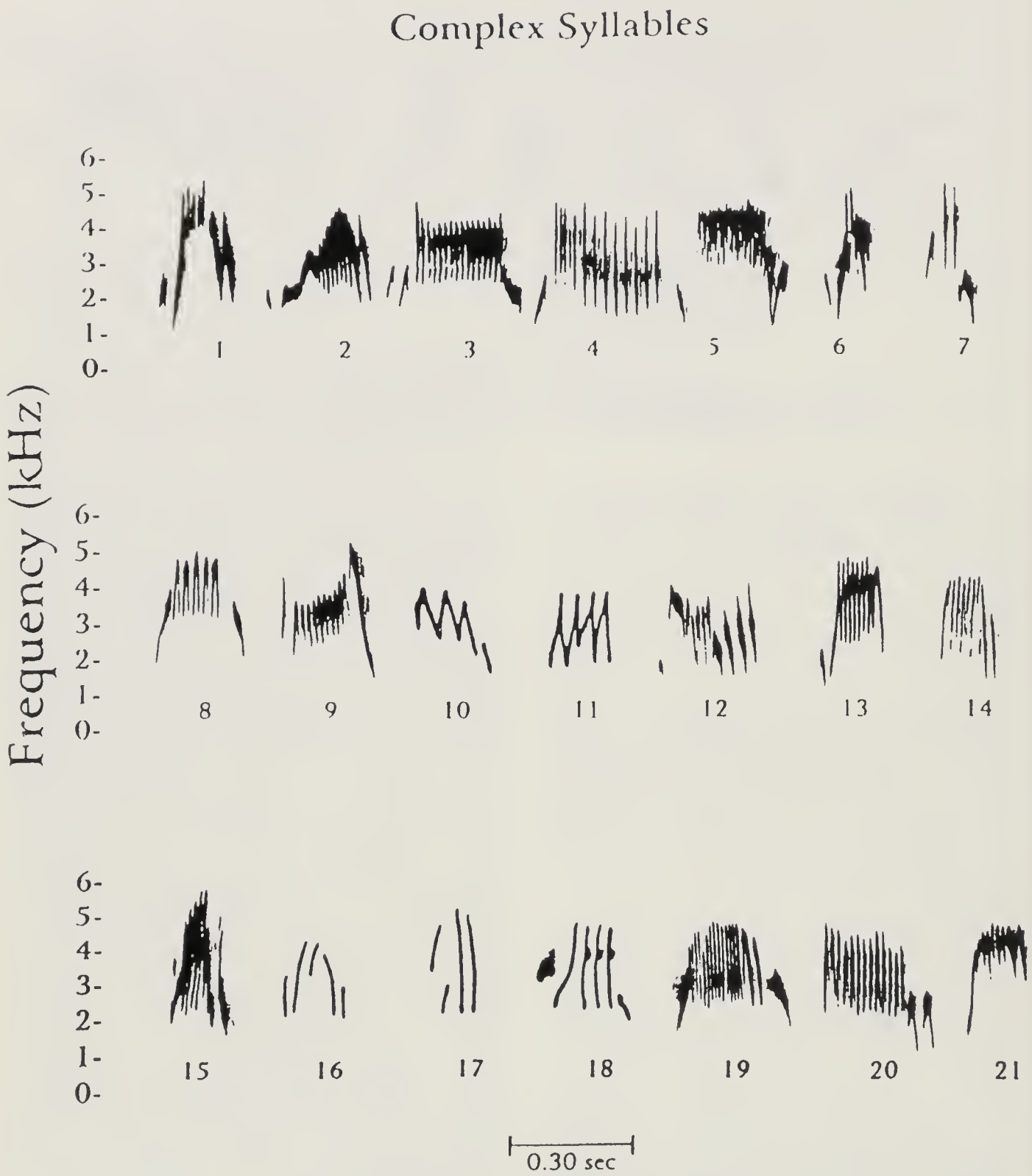

FIG. 4. Complex syllables of Northern Parula type B songs. Syllable types 1, 3, 5, 10, 11, and 20 from eastern birds only, while variants 14, 16, 17, and 18 from western birds only.

another used CS_4 and TS_7). It is unknown whether individuals with the same song (i.e., same phrase and syllables) within a specific locality were neighbors because most of these songs were not recorded by the author. It is likely that some of these individuals were members of the same local population because many of these songs were recorded within the same year. Some morphological differences were evident in specific syllable types between individuals (e.g., CS_{13} might differ slightly between two birds; Fig. 7). Morphological differences in simple syllables were evident between those used in the middle of

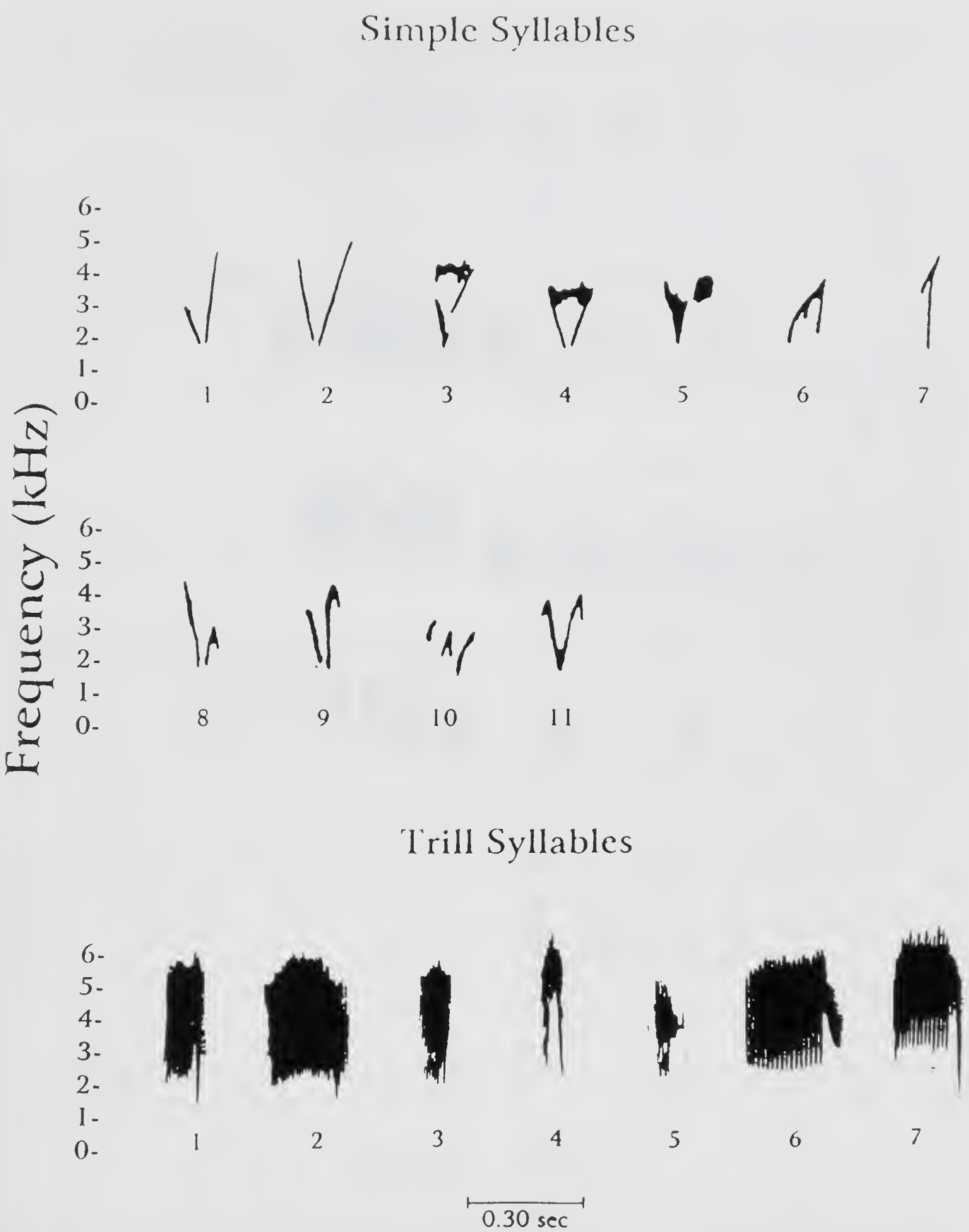

FIG. 5. Simple and trill syllables of Northern Parula type B songs. Simple syllable types 1, 3, and 5 and trill syllable type 6 from western birds only.

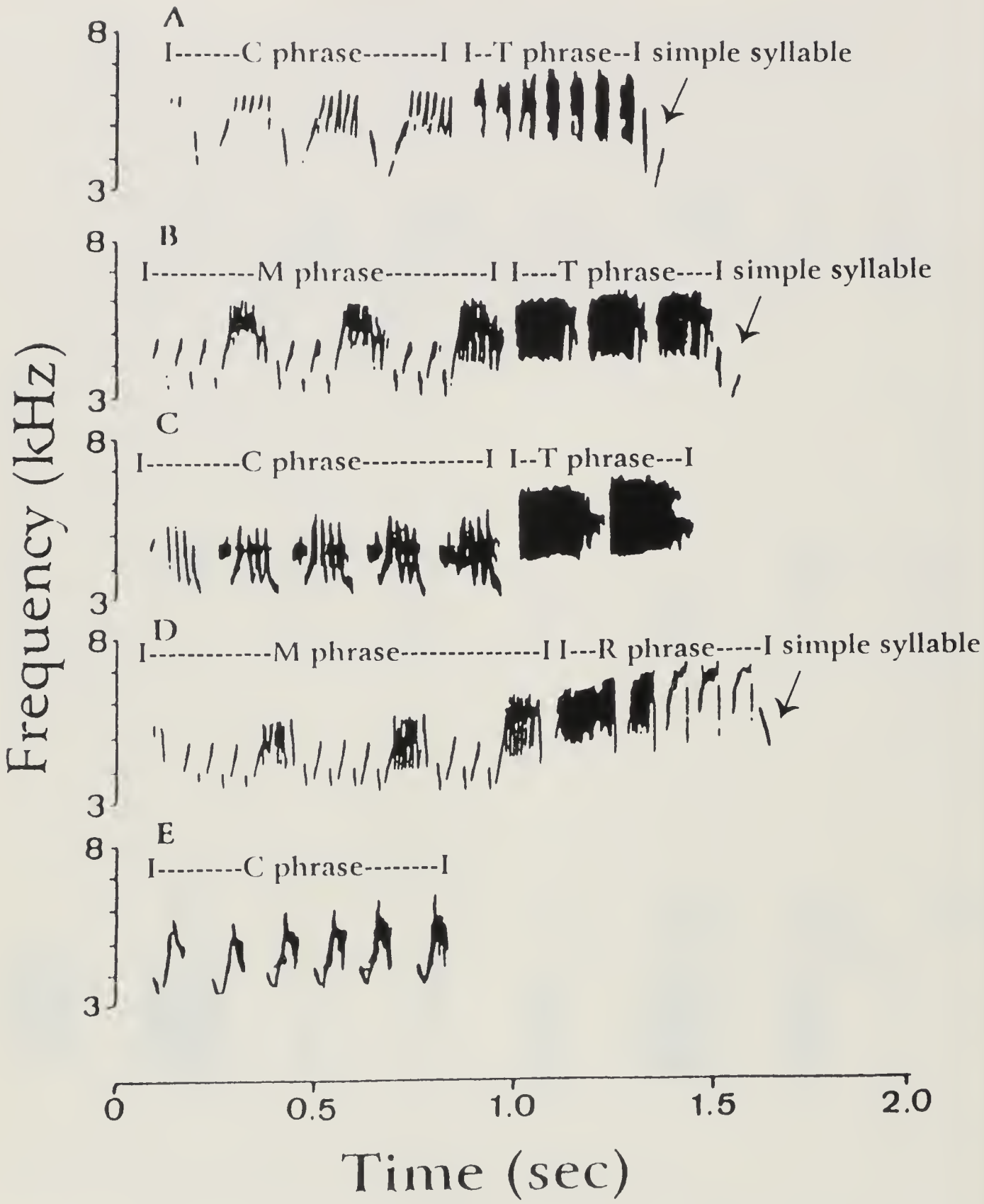

FIG. 6. The five most common song or phrase patterns observed in Northern Parula type B songs. (A) pattern C-T-SS [67% of all songs (west = 0.0%, southeast = 92%, northeast = 100%)], (B) pattern M-T-SS [13.1% of all songs (west = 45.0%, southeast = 0.0%, northeast = 0.0%)], (C) pattern C-T [6.2% of all songs (west = 17%, southeast = 2.6%, northeast = 0.0%)], (D) pattern M-R-SS [3.6% of all songs (west = 12.1%, southeast = 0.0%, northeast = 0.0%)], (E) pattern C [2.1% of all songs (west = 2.4%, southeast = 4.1%, northeast = 0.0%)].

TABLE 1. A comparison of song variables from western, southeastern, and northeastern type B songs of the Northern Parula (values are mean ± SD). Number of individuals in which songs were analyzed: West = 41, Southeast = 38, Northeast = 41.

Variable	Song population			ANOVA *F*-value[c]
	West	Southeast	Northeast	
Song duration (s)[a]	1.5 ± 0.2	1.4 ± 0.2	1.3 ± 0.1	10.90**
Number of syllables	11.9 ± 2.9	11.3 ± 3.1	11.4 ± 2.7	0.53
Syllable types in a song	4.0 ± 1.3	3.7 ± 1.0	3.6 ± 0.5	1.26
Maximum frequency (kHz)[a]	7.0 ± 0.4	7.2 ± 0.4	6.6 ± 0.4	4.31*
Minimum frequency (kHz)	4.4 ± 0.5	4.4 ± 0.5	4.2 ± 0.4	2.10
Complex syllables[a,b]	3.7 ± 1.6	3.5 ± 1.3	3.4 ± 0.9	0.71
Simple syllables[a,b]	4.6 ± 3.0	1.1 ± 1.0	1.0 ± 0.3	16.3***
Trill syllables[a,b]	2.9 ± 1.5	5.1 ± 2.6	6.5 ± 2.7	23.9***

[a] Multiple Comparison (Bonferroni Correction; $\alpha = 0.05$): Song Duration (W ≠ Se = Ne), Maximum Frequency (W = Se ≠ Ne), Simple Syllables (W ≠ Se = Ne), Trill Syllables (W ≠ Se ≠ Ne).
[b] Number per song.
[c] * $P < 0.025$, ** $P < 0.001$, *** $P < 0.0005$.

the song (to form M phrases) versus the single simple syllable terminating the song (as usually occurs in most parula B songs).

DISCUSSION

Song structure.—Northern Parula B songs are complex and show much intraspecific variation. Song complexity occurs because most songs contain multiple phrases (usually two) that vary in syllable types between individuals. A similar arrangement occurs in B songs of the Grace's Warbler (*Dendroica graciae*; Staicer 1989) and the type II song of the Blue and Golden-winged warblers (Gill and Murray 1972, Highsmith 1989). Some evidence suggests that complexity in B songs may be a result of intrasexual usage (e.g., territorial clashes between males), while A songs, used for mate attraction, are more stereotyped (Kroodsma 1981).

Geographic variation.—Northern Parula type A songs are very similar in most variables (except trill rate, frequency, and song length), but differ significantly between eastern and western populations in the type of terminal syllable (Moldenhauer 1992). Males from each population recognize and respond differentially to the two types of A songs (Regelski and Moldenhauer 1996). Similarly, the type B song exhibited differences between eastern and western populations in song length and maximum frequency, but primarily differed in the number of specific syllable types and phrase patterns composing songs. For instance, western birds frequently used more simple syllables per song and often used these syllables to construct the M phrase pattern, which was absent from eastern singers.

Moldenhauer (1992) argued for subspecific recognition of *P. americana* (*P. a. americana* for the east and *P. a. ludoviciana* for the west) based upon the terminal note difference in the type A songs. Results from my study are consistent with this division, based upon B song phrase patterning between eastern and western populations. The terminal note in the type A song is readily identifiable both audibly and visually by sonogram. Likewise, B songs with M phrases (western population) may be audibly distinguished from songs without M phrases (eastern population); they are longer (composed of more syllables) and more buzzy. These differences are easily viewed by comparing sonograms (Fig. 6B, D vs Fig. 6A, C). Whether these structural differences in eastern and western type A and B songs are influenced by learning and/or have a genetic basis has yet to be determined.

Populations from each geographic region contained a repertoire of unshared syllables (15.3% confined to the eastern population, 20.5% confined to the western population); however, many (57%) were shared. Syllable confinement within specific macrogeographical areas reported in my study might be viewed with some speculation. For instance, some individual songs contained more than one syllable type within a syllable class, particularly trill and simple syllables. No individ-

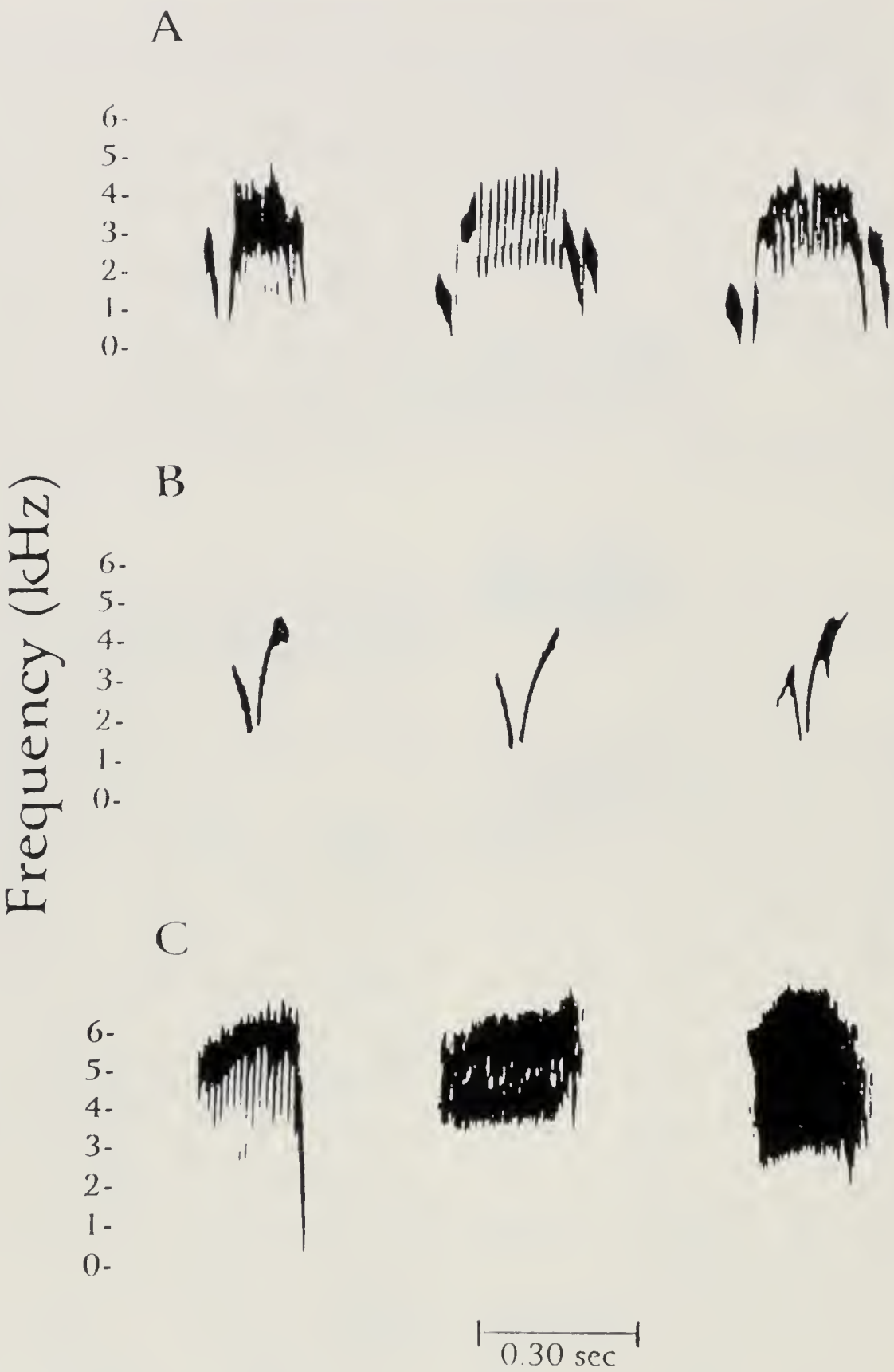

FIG. 7. Examples of morphological variations of specific syllable types between individuals (A) CS_{13} (complex syllable), (B) SS_1 (simple syllable), (C)TS_2 (trill syllable).

uals for which multiple songs were examined sang more than 1 complex syllable type. However, because of the small sample size (only 5 individuals recorded with at least 5 songs from each), these results should be viewed with caution. Within specific microgeographic areas, syllable sharing could be variable even though a few individuals sang some or all of the same syllables.

In other warbler species that have a song similar to the type B of the Northern Parula, local dialect patterns are usually evident, which suggests that young males learn B songs from neighboring conspecifics (Kroodsma 1981). Thus an individual from an area that contains a song similar to his neighbors, will be more effective during countersinging bouts (Kroodsma 1981). Playback experiments show that Blue-winged Warbler males respond more intensely to their local type II (B) songs but do not differentiate among type I (A) songs of different localities (Kroodsma et al. 1984). Although Northern Parula B songs tend to be complex and differ between locations (in either phrase pattern or syllable types used), Bay (1987) found no discernable patterns or dialects in songs from the two best sampled areas (representing 10 and 15 individuals) in Texas.

Future studies should concentrate on gathering information concerning site fidelity in successive breeding years to allow a better understanding of type B song structure at the microgeographic level. Such data might also reveal whether young males learn the same types of syllables and phrase patterns in successive years or different ones as a result of the exposure to new individuals. In addition, researchers should determine what role, if any, the disjunct winter distribution of the Northern Parula has on song learning and the geographical differences in the type A and B songs on the breeding grounds

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APPENDIX

Recording localities for Northern Parula type B songs. Localities are listed by geographic region and then alphabetically by state (or country) and county, parish, or province. Number of individuals per locale are indicated in parenthesis.

Southeast region.—Alabama: Dale (1), Dallas (1), Clark (1), Covington (2), Monroe (2), Wilcox (4). Florida: Alatchua (1), Dade (3), Flager (1), Jefferson (2), Polk (1), Wakulla (1). Georgia: Bulloch (3), Chatham (4), Jenkins (6), Richmond (1). North Carolina: New Hanover (3). South Carolina: Richland (8). Tennessee: Dickson (1), Sevier (1).

Northeast region.—Canada: Gaspe (1). Maine: Lincoln (44). Ohio: Franklin (2), Seneca (1). West Virginia: Monogalia (1).

West region.—Lousiana: St. Tammany (2). Mississippi: George (3), Hancock (4). Texas: Hardin (2), Montgomery (2), Trinity (2), Walker (25).

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NESTING BIOLOGY OF DICKCISSELS AND HENSLOW'S SPARROWS IN SOUTHWESTERN MISSOURI PRAIRIE FRAGMENTS

MAIKEN WINTER[1,2]

ABSTRACT.—According to data from the North American Breeding Bird Survey, populations of Dickcissel (*Spiza americana*) and Henslow's Sparrow (*Ammodramus henslowii*) have declined severely during the last 30 years. The reasons for their population declines seem to differ; habitat fragmentation on the breeding grounds has been suggested to have little negative impact on Dickcissels, but appears to be a major reason for Henslow's Sparrow declines. Previous reports on the status of Dickcissels and Henslow's Sparrows largely were based on density estimates without considering the nesting biology of the two species. My comparison of the nesting biology of Dickcissel and Henslow's Sparrow provides some insight into potential factors that might contribute to their population declines. During 1995–1997, I studied the nesting biology of Dickcissels and Henslow's Sparrows in fragments of native tallgrass prairie in southwestern Missouri. Both species had similar clutch sizes, rates of hatching success, and numbers of young fledged per successful nest. Dickcissels tended to have lower rates of nesting success and higher rates of brood parasitism by Brown-headed Cowbirds (*Molothrus ater*) than Henslow's Sparrows. Although several vegetation characteristics at the nest differed between successful and depredated nests in Dickcissels, no differences were found between successful and depredated Henslow's Sparrow nests or between parasitized and unparasitized Dickcissel nests. My results indicate that Dickcissels might reproduce less successfully than Henslow's Sparrows in southwestern Missouri, and might therefore be of higher conservation concern on the breeding ground than previously thought. *Received 27 January 1999, accepted 3 June 1999.*

Data from the North American Breeding Bird Survey indicated that populations of Dickcissel (*Spiza americana*) and Henslow's Sparrows (*Ammodramus henslowii*) have declined by about 39% and 91%, respectively, during the last 30 years (Peterjohn et al. 1994). The reasons for the declines are thought to differ between the two species: Dickcissels are assumed to have declined mainly because of poisoning on their South American wintering grounds (Basili and Temple 1995, Basili 1997), and are thought to be little affected by breeding habitat loss or fragmentation (Herkert et al. 1993). In contrast, the population decline of Henslow's Sparrows seems to be mainly caused by loss and fragmentation of suitable grassland habitat on their breeding grounds (Herkert 1994). However, status assessments of Dickcissels and Henslow's Sparrows are based largely on estimates of density or relative abundance, without considering the breeding ecology of the two species. A comparison of the breeding ecology of Dickcissels and Henslow's Sparrows might provide information on factors that could cause differential reproductive success in the two species. Such factors might include clutch sizes, rates of brood parasitism by Brown-headed Cowbirds (*Molothrus ater*), rates of nest predation, and hatching and fledging rates. Vegetation characteristics at the nest site might differ between the species and cause one species to be more susceptible to nest predation or cowbird parasitism.

In southwestern Missouri, little information has been collected on the nesting success of passerines breeding in tallgrass prairie fragments. In this study I describe and compare nesting characteristics of the Dickcissel and the Henslow's Sparrow in fragments of native tallgrass prairie in southwestern Missouri between 1995 and 1997. Detailed analyses on the effect of fragment size, proximity to habitat edge, management practices, and landscape structure on density and nesting success of these species are described elsewhere (Winter 1998, Winter and Faaborg in press).

Dickcissel.—Dickcissels are grassland habitat generalists; they can be found breeding in a wide variety of grassland vegetation (Bent 1968). Because males often sing from elevated perches and females often place their nests above the ground, they tolerate a relatively

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large number of shrubs and trees. As with most polygynous species, the female generally tends both eggs and young alone.

In spite of their ability to use secondary habitats such as non-native grasslands or road right-of-way, Dickcissel populations have declined by about 39% since 1966 (Peterjohn et al. 1994). Population trends in Dickcissels are difficult to estimate because their abundance and distribution fluctuate considerably among years (Fretwell 1986), but habitat fragmentation did not seem to be responsible for their population declines (Herkert et al. 1993). Instead, poisoning of tens of thousands of birds on the wintering grounds has been suggested as cause for its population decline (Basili and Temple 1995, Basili 1997). Recent evidence indicates that habitat fragmentation on the breeding grounds might also have a negative impact on this species (Winter 1998, Winter and Faaborg in press).

Henslow's Sparrow.—Little is known about the nesting behavior of this inconspicuous species because of its furtive behavior and its tendency to spend most of its time on the ground (Bent 1968). Its highest densities occur in grasslands with tall, dense vegetation and a well-developed layer of litter (Wiens 1969, Robins 1971, Zimmerman 1988, Herkert 1994, Mazur 1996, Winter 1998). Based on the few existing nesting studies (Hyde 1939, Bent 1968, Robins 1971, Schulenberg et al. 1994, Rohrbaugh et al. in press), we know that this monogamous species generally nests close to the ground in tall dense vegetation, preferably within large clumps of litter.

With the destruction of tallgrass prairie and similar grassland habitats, the breeding range of Henslow's Sparrows has contracted considerably during the last 30 years, mainly in the northeastern, eastern, and northwestern parts of its range (Pruitt 1996). Although Henslow's Sparrows also nest in secondary habitats such as hayfields and reclaimed surface mines (see review in Swanson 1996), it has shown a consistent population decline (Peterjohn et al. 1994, Herkert 1997). Analysis of Christmas Bird Count data in the southeastern United States also indicates population declines on the wintering grounds (Butcher and Lowe 1990). The major reason for the large population decline of Henslow's Sparrows has been suggested to be loss and fragmentation of habitat on the breeding grounds (Herkert 1994). However, studies in Missouri, Kansas, and Ohio indicated that Henslow's Sparrows can occurr in even small fragments (see Winter 1998), and since 1988 its populations have been steadily increasing in Illinois (J. R. Herkert, pers. comm.).

STUDY SITES AND METHODS

Study area.—Between 1995 and 1997, I studied the nesting biology of Dickcissels and Henslow's Sparrows in 13 fragments of native tallgrass prairie in southwestern Missouri (approx. 37° 30′ N, 93° 30′ W; Winter 1998). Dominant grasses in the study area included big bluestem (*Andropogon gerardii*), little bluestem (*Schizochyrium scoparium*), and Indian grass (*Sorghastrum nutans*). Dominant forbs included sunflower (*Helianthus* spp.), milkweed (*Asclepias* spp.), blazing star (*Liatris spicata*), and sensitive briar (*Schrankia nuttallii*). Prairies were owned by the Missouri Department of Conservation, the Missouri Prairie Foundation, The Nature Conservancy, and the Missouri Department of Natural Resources and were actively managed by prescribed burning and haying (see Winter 1998).

Nest searching and monitoring.—Throughout each field season (early May to end of July) my field assistants and I located and monitored nests of all grassland species that we found, but focused our nest searching efforts on finding nests of Henslow's Sparrows and Dickcissels. Nests were found by walking across the study sites and adjacent areas of similar vegetation, while paying close attention to behavior and vocalizations of nearby adult birds. Most nests were found by observing adults (Dickcissels: 80%; Henslow's Sparrows: 56%). Behavioral patterns of adults that we used as clues that nests might be nearby were chipping, flying short distances away or around the observer, flushing close to the observer followed by a short flight, and carrying nest material, fecal sacs, or food. The location of a potential nest site was marked with a short length of flagging tape at three locations within 1 m of a potential nest site forming a triangle. We then retreated 10–30 m and tried to locate the nest when the bird returned. Nests also were located by flushing birds while randomly walking across the prairie (Dickcissel: 10%; Henslow's Sparrow: 30%). The remaining 10% and 14% of all nests, respectively, were found fortuitously; flushing birds while doing other research activities such as vegetation measurements or censusing. Because rope-dragging and systematic search were ineffective methods for nest finding in 1995, I did not use those methods in the following years.

We did not search for or monitor nests when vegetation was wet (after rain or heavy dew immediately after sunrise) to minimize disturbance of vegetation surrounding nests. Each nest was marked with a flag 5 m to the north and a small ribbon was placed about 30 cm south of those nests that were hard to find. Every 3–4 days nest fate was checked by walking past

the nest to avoid creating "dead ends" that might lead nest predators to the nest. During each nest check we recorded the number of host and cowbird eggs and young, presence or absence of adults, and the state of the nest if the nest was found empty. An empty nest was considered successful if one or more of the following cues were observed: feces in the nest, feather sheaths in the nest, nest rim flattened, adults carrying food or chipping, or fledgling close to nest.

Nest vegetation.—Nest vegetation was characterized within one week after activity at a nest had ceased. Vegetation was measured at five locations around the nest site: directly at the nest and 0.5 m from the nest in each cardinal direction. At each of the five points I measured vegetation cover (Daubenmire 1959), the number of woody stems within each Daubenmire frame, vegetation height, litter depth, and visual obstruction (Robel et al. 1970; for a more detailed description see Winter 1998). For each nest I calculated the mean for each of the five measuring points, and used the mean of those five data points for further analysis.

Estimates of nesting success.—When calculating rates of nesting success, I excluded nests for which it was not possible to determine if predation happened before or after a nest was abandoned. This was true for nests that had small clutch sizes (1–2 eggs) and were depredated the next time the nest was checked. Those nests, however, were included for estimating rates of cowbird parasitism. For each year I estimated species specific probabilities of daily nest survival (Mayfield 1975) separately for incubation and nestling stages, and for the total nesting period. The total probability of nest survival was defined as the probability that a nest successfully survived incubation and nestling periods and fledged at least one young of the parental species. In the two species that I investigated, incubation begins with the laying of the last egg (Bent 1968). I used the following exponents to estimate the probability of nesting success over the entire nesting period: Dickcissel: 21 days (12 incubation days plus 9 nestling days), and Henslow's Sparrow: 20 days (11 incubation days plus 9 nestling days; Ehrlich et al. 1988). Standard errors for daily nest survival rates were calculated by using the formula for binomial distributions (Zar 1996). I used means and confidence intervals (Johnson 1979) to compare rates of nesting success among years and between incubation and nestling stages in each year. To allow comparison with other studies that did not use Mayfield estimates, I also present the apparent proportion of successful nests.

Statistical analyses.—Logistic regression was used to investigate if nesting success was related to the date in the breeding season. I calculated mean clutch size for each week in the breeding season and used linear regression analysis to investigate if clutch size varied during the nesting season. Because the number of nests found varied among weeks, I weighted the mean weekly clutch size by its standard error. For this analysis I used all unparasitized nests of the three years of the study.

Vegetation characteristics of depredated and successful Dickcissel and Henslow's Sparrow nests were compared with a two-tailed *t*-test. *P*-values were compared to the *P*-values obtained from a sequential Bonferroni adjustment (Rice 1989). The same analysis was used to compare characteristics between Dickcissel and Henslow's Sparrow nests. Dickcissel was the only species with enough parasitized nests to allow for statistical analysis. For this species, host clutch size, number of host fledglings, and nest characteristics of parasitized and unparasitized nests were compared with *t*-tests. Nesting success of unparasitized and parasitized Dickcissel nests were compared by using means and confidence intervals (Johnson 1979). Logistic regression was used to investigate if cowbird parasitism was related to the date in the breeding season. All data were analyzed with SAS (SAS 6.03 for PC; SAS Institute, Inc. 1988) and are presented as means and standard errors; the level of significance was set at 0.05.

RESULTS

Nesting biology.—Henslow's Sparrows typically arrived in the study area in early May, about 1–2 weeks earlier than most Dickcissels, and stopped nesting by the end of July, also about 1–2 weeks earlier than most Dickcissels (Fig. 1). The latest observed initiation of incubation in Henslow's Sparrows was 16 July. In contrast to Henslow's Sparrows, some Dickcissels were observed carrying nesting material in early August. Although most Dickcissels seem to have completed their nesting activity by the end of July, some might nest until the end of August. The peak of Dickcissel nest initiation did not occur until early June, and they continued to nest throughout June and early July (Fig. 1A). In contrast to Dickcissels, Henslow's Sparrows had two peaks of nest initiation, one in the second and third week of May, and one in the middle of June (Fig. 1B).

Dickcissels and Henslow's Sparrows had almost identical clutch sizes, hatching and fledging rates, and lengths of nestling stages (Table 1). Clutch size of Dickcissels and Henslow's Sparrows tended to decline with date in the breeding season but not significantly (Dickcissel: $F = 4.8$, $r^2 = 0.35$, df = 9,10, $P = 0.06$, slope = -0.05 ± 0.02; Henslow's Sparrow: $F = 5.0$, $r^2 = 0.38$, df = 8,9, $P = 0.06$, slope = -0.05 ± 0.02).

Nesting success.—The main cause of nest failure was nest predation; 86% of all failed Henslow's Sparrow nests and 84% of all failed Dickcissel nests were depredated (Table

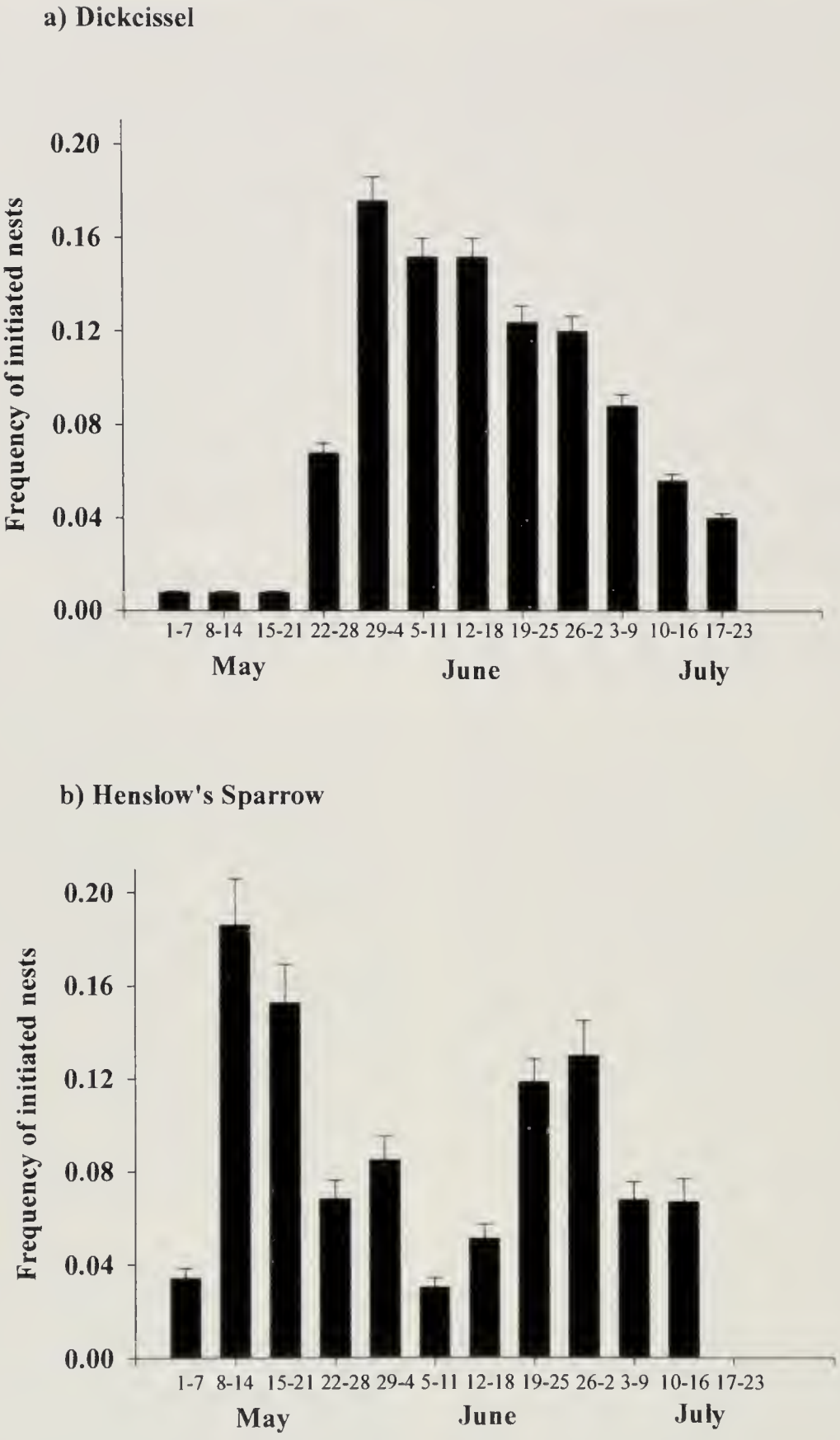

FIG. 1. Frequency distribution of clutch initiation dates in (A) Dickcissels and (B) Henslow's Sparrows in southwestern Missouri, 1995–1997.

1). Nest failure from unknown causes (probably weather) or nest abandonment were minimal (Table 1). None of the nests of either species failed as a result of cowbird parasitism. Dickcissel nesting success was lower during incubation than during the nestling stage in 1996, whereas nesting success during incubation and nestling stages did not differ

TABLE 1. General nesting data ($\bar{x} \pm$ SE) of Dickcissel and Henslow's Sparrow in southwestern Missouri prairie fragments, 1995–1997.

	Dickcissel (n = 242)[a]	Henslow's Sparrow (n = 59)
General nesting data:		
Successful nests (n)	112	34
Depredated nests (n)	128	25
Unknown loss (n)	2	0
Abandoned nests (n)[b]		
a) during nest building	13	0
b) with eggs	2	1
c) parasitized	3	0
Mowed nests (n)[c]	4	3
Nesting success:		
Mayfield nesting success (%)[d]	29.7	39.5
Apparent nesting success[e]	46.3	57.6
Nesting biology:		
Clutch size (n)[f]	3.9 ± 0.05 (227)	3.8 ± 0.10 (56)
Incubation days (n)[g]	11.45 ± 0.08 (11)	12.0 ± 0 (1)
Nestling days (n)[h]	8.7 ± 0.02 (52)	9.1 ± 0.08 (9)
Hatching success (n)[i]	92.9 (69)	93.2 (12)
Young fledged/nest	1.7	2.0
Young fledged/successful nest	3.6	3.5
Broad parasitism:		
Parasitized nests (%)[j]	8.8 ± 0.005 (21)	5.3 ± 0.006 (3)
Young fledged from successful unparasitized nests	3.7 ± 0.13 (105)	3.6 ± 0.25 (33)
Young fledged from successful parasitized nests	2.3 ± 0.26 (6)	2.0 ± 0 (1)

[a] Total number of nests found excluding those that were abandoned and mowed.
[b] Not included in the total number of nests.
[c] Not included in the total number of nests.
[d] After Mayfield (1975).
[e] Percent of successful nests from all nests found.
[f] Only unparasitized nests were used.
[g] n = number of nests that could be followed from nest building until hatching.
[h] n = number of nests that could be followed from hatching until fledging.
[i] Percent hatched eggs from all eggs for which the clutch size was known with certainty (see Methods).
[j] Percent of parasitized nests out of all nests found.

significantly in any other year or for Henslow's Sparrows (Table 2). Nesting success did not vary significantly with the date in the breeding season for either Dickcissels (Wald-$\chi^2 = 0.22$, $P > 0.05$, $n = 240$) or Henslow's Sparrows (Wald-$\chi^2 = 2.66$, $P > 0.05$, $n = 59$). Dickcissel nesting success was higher in 1997 than in 1996, whereas nesting success of Henslow's Sparrows did not vary significantly among years (Table 2). Mayfield nesting success tended to be higher in Henslow's Sparrows (40%) than in Dickcissels (30%; Tables 1, 2); however, the 95% confidence intervals for the estimates of nesting success in these two species overlapped.

Cowbird parasitism.—The rate of brood parasitism by Brown-headed Cowbirds was low, but slightly higher in Dickcissels (9.6%) than in Henslow's Sparrows (5.3%; Table 1). Dickcissel nests were parasitized throughout the nesting season except for the first and third week of May and the last week of July (Fig. 2).

Parasitized nests generally had smaller clutches, fewer fledglings, and lower nesting success than unparasitized nests (Table 3). On average, cowbirds laid 1.4 eggs per parasitized Dickcissel nest. None of the three parasitized Henslow's Sparrow nests had more than one cowbird egg. Host clutch size in both species was reduced by about 0.9 eggs per parasitized nest (Table 3). The reduction in clutch size was significant in Dickcissels ($t = 4.07$, df = 23, $P < 0.001$), with fewer host

TABLE 2. Nesting success of Dickcissel and Henslow's Sparrow in southwestern Missouri prairie fragments, 1995–1997.

Year	Nest cycle interval	n[a]	Depredated (n)[b]	Exposure days[c]	Survival ± SE[d]	Success (%)[e]
Dickcissel						
1995	Incubation	9	4	69.0	0.94 ± 0.03	21.6 < 48.8 < 100
	Nestling	12	4	74.5	0.95 ± 0.03	35.0 < 60.8 < 100
	Total[f]	18	8	143.5	0.94 ± 0.02	10.9 < 30.0 < 65.0
1996	Incubation	82	44	511.5	0.91 ± 0.01	24.7 < 34.0 < 44.5[g]
	Nestling	61	19	388.5	0.95 ± 0.01	52.0 < 63.7 < 76.0[g]
	Total	113	67	900.0	0.92 ± 0.01	12.0 < 19.7 < 24.9[g]
1997	Incubation	90	32	517.0	0.94 ± 0.01	36.8 < 46.4 < 61.3
	Nestling	98	30	618.0	0.95 ± 0.01	53.0 < 63.9 < 74.6
	Total	117	53	1235.0	0.96 ± 0.01	32.6 < 39.8 < 55.1[g]
All[h]	Incubation	181	80	1097.5	0.93 ± 0.01	34.0 < 40.3 < 51.4
	Nestling	171	53	1081.0	0.95 ± 0.01	46.4 < 63.6 < 70.6
	Total	248	128	2278.5	0.94 ± 0.00	21.8 < 29.7 < 34.0
Henslow's Sparrow						
1995	Incubation	6	0	34.5	1.0 ± 0.00	100.0
	Nestling	7	2	59.0	0.97 ± 0.02	52.0 < 73.3 < 100
	Total	7	2	83.5	0.98 ± 0.02	29.0 < 66.8 < 100
1996	Incubation	11	5	103.5	0.95 ± 0.02	35.4 < 58.0 < 89.5
	Nestling	16	8	146.0	0.94 ± 0.02	38.7 < 60.2 < 83.4
	Total	21	13	249.5	0.95 ± 0.01	23.4 < 34.3 < 54.4
1997	Incubation	14	4	84.5	0.95 ± 0.02	35.4 < 58.7 < 89.5
	Nestling	26	6	133.0	0.95 ± 0.02	42.8 < 66.0 < 91.0
	Total	31	10	217.5	0.95 ± 0.01	23.4 < 39.0 < 54.0
All	Incubation	31	9	222.5	0.96 ± 0.01	50.6 < 63.5 < 80.1
	Nestling	49	16	334.0	0.95 ± 0.01	52.0 < 64.3 < 76.0
	Total	59	25	550.5	0.95 ± 0.01	24.4 < 39.5 < 52.2

[a] Total number of nests monitored in a specific nesting interval during incubation and nestling stages. Because nests were mostly monitored during parts of both nesting stages, the sum of nests in each interval is higher than the total number of nests found.
[b] Total number of depredated nests.
[c] Total number of exposure days (Mayfield 1975).
[d] Probability of daily Mayfield nesting success (Day) = − (# depredated nests/# Mayfield days) + 1 SE = sqrt ((Day * (# depredated nests/# Mayfield days))/# Mayfield days).
[e] Probability of nesting success over the entire interval = $\text{Day}^{\text{interval length}}$, shown are means and lower and upper 95% confidence intervals (Johnson 1979).
[f] Both nesting stages combined.
[g] Intervals with the same letter do not overlap.
[h] All years combined.

young fledged from successful parasitized nests (t = 4.10, df = 34, $P < 0.001$). The reduction in nesting success was not caused by competition with cowbird young, but rather by a higher predation rate on parasitized nests; all successful parasitized nests fledged young of both host and cowbird.

Nest characteristics.—Compared to Henslow's Sparrows, Dickcissels chose a variety of nest sites. Most (45%) nests were placed in forbs, especially leadplant (*Amorpha canescens*) and ashy sunflower (*Helianthus mollis*), but shrubs (29%), grass (16%), and litter (10%) also were used as nesting substrates. Nests were typically woven in the stems of forbs or woody plants. Because nest searches were restricted to grassland habitat, nests were not found within shrubby edge habitats. However, many Dickcissels were observed breeding in such edge habitats (Winter 1998). Successful nests had taller vegetation, greater visual obstruction values, greater coverage by grass, and smaller areas of bare soil than unsuccessful nests (Table 4). None of the vegetative characteristics that I measured at Dickcissel nest sites differed between parasitized and unparasitized nests (Table 4).

Henslow's Sparrows typically placed their nests among layers of thick litter (82% of all nests). Compared to Dickcissel nests, the vegetation surrounding Henslow's Sparrow nests had deeper litter (3.5 ± 0.27 vs 1.9 ± 0.23

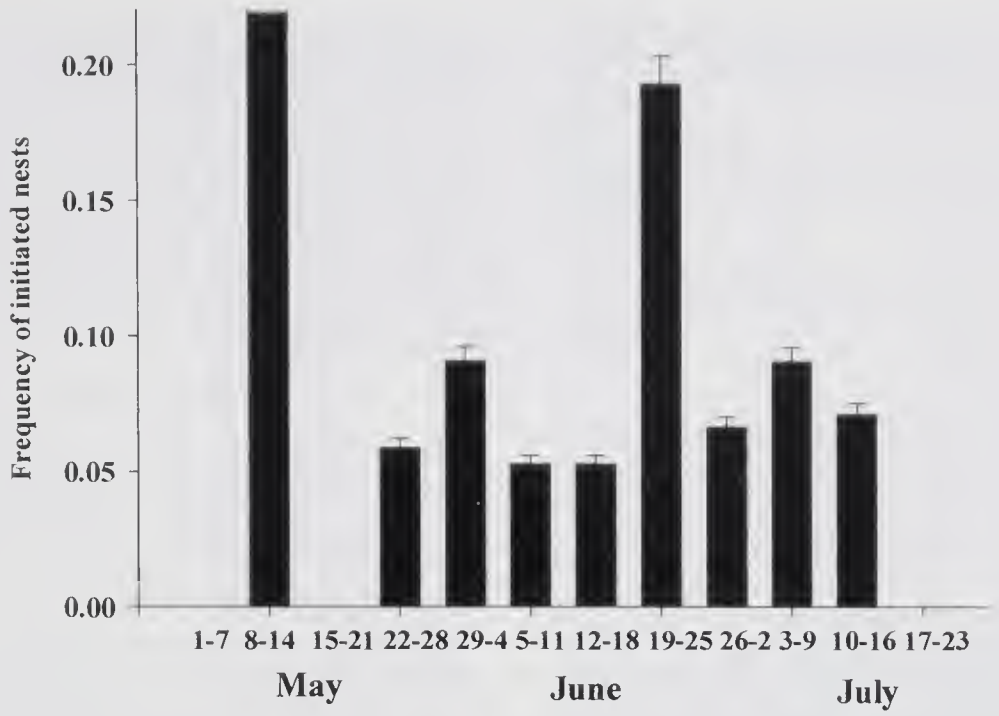

FIG. 2. Frequency distribution of rates of cowbird parasitism on Dickcissel nests in southwestern Missouri, 1995–1997.

cm; $t = 3.3$, df = 296, $P = 0.001$), lower vegetation (42.0 ± 1.12 vs 46.1 ± 0.67 cm; $t = -2.8$, df = 296, $P = 0.005$), greater cover by litter (29.6 ± 2.0 vs 11.6 ± 0.71%; $t = 10.4$, df = 296, $P < 0.001$), and less cover by forbs (17.9 ± 1.03 vs 26.0 ± 0.83%; $t = -4.6$, df = 296, $P < 0.001$), woody plants (1.5 ± 0.12 vs 5.2 ± 0.62%; $t = -2.9$, df = 296, $P = 0.004$), and soil (0.4 ± 0.12 vs 4.8 ± 0.40%; $t = -5.5$, df = 296, $P < 0.001$). Henslow's Sparrow nests also had a higher percentage of nest cover (90.3 ± 2.68 vs 67.7 ± 1.79%; $t = 5.9$, df = 296, $P < 0.001$), and were located closer to the ground (7.2 ± 0.53 vs 18.4 ± 1.04 cm; $t = -5.4$, df = 134, $P < 0.001$). All significant P-values remained significant after a sequential Bonferroni adjustment. Henslow's Sparrows were never observed to place their nest within or in immediate proximity to woody vegetation. In contrast to Dickcissels, Henslow's Sparrows did not weave their nests into the surrounding vegetation, but placed them loosely among the surrounding stems of grass and dead vegeta-

TABLE 3. Clutch size ($\bar{x}$ ± SE) and nesting success of unparasitized and parasitized nests in Dickcissel and Henslow's Sparrow in southwestern Missouri, 1995–1997.

	Unparasitized nests					Parasitized nests					
Year	*n*	Clutch size	Exposure days	Failed nests	Success[a] (%)	*n*	Host clutch	Cowbird clutch	Exposure days	Failed nests	Success (%)
Dickcissel											
1995	17	3.9 ± 0.13	143.5	7	35.0	1	3.0 ± 0	2.0 ± 0	12.0	1	16.1
1996	104	3.9 ± 0.07	931.0	62	23.5	5	3.4 ± 0.40	2.0 ± 0.55	26.0	5	1.1
1997	98	3.9 ± 0.07	1014.5	44	39.4	15	3.0 ± 0.26	1.2 ± 0.14	152.0	9	27.7
All	220	3.9 ± 0.05	2089.0	113	31.2	21	3.0 ± 0.22	1.4 ± 0.18	190.0	15	17.8
Henslow's Sparrow											
1995	6	4.3 ± 0.21	79.0	2	59.9	1	3.0 ± 0	1.0 ± 0	15.0	0	100
1996	21	3.7 ± 0.17	138.0	13	13.8	0	N/A	0	N/A	N/A	N/A
1997	29	3.7 ± 0.15	201.5	8	44.5	2	3.0 ± 0	1.0 ± 0	16.5	2	7.5
All	56	3.8 ± 0.10	418.5	23	32.3	3	3.0 ± 0	1.0 ± 0	31.5	2	26.9

[a] Probability that a nest survived both incubation and nesting periods, estimated after Mayfield (1975).

TABLE 4. Dickcissel nest characteristics ($\bar{x} \pm$ SE) in successful and depredated nests, and non-parasitized and parasitized nests in southwestern Missouri prairie fragments, 1995–1997. All significant *P*-values remained significant after a Bonferroni adjustment.

	Nest success					Nest parasitism				
Variable	Successful (n = 106)	Depredated (n = 109)	t	df	P	Unparasitized (n = 197)	Parasitized (n = 18)	t	df	P
Litter depth (cm)	2.0 ± 0.22	1.5 ± 0.19	−1.6	213	0.11	1.8 ± 0.15	1.4 ± 0.41	0.8	213	0.40
Vegetation height (cm)	48.9 ± 0.85	44.4 ± 1.03	−3.4[a]	209	<0.001	46.8 ± 0.72	43.9 ± 2.16	1.1	213	0.25
Visual obstruction (dm)	29.6 ± 0.80	25.9 ± 1.13	−2.7[a]	195	<0.008	27.8 ± 0.69	26.6 ± 4.02	0.3[a]	18	0.77
No. woody stems	0.4 ± 0.08	0.6 ± 0.11	1.3[a]	203	0.18	0.5 ± 0.07	0.7 ± 0.24	−0.8	215	0.44
Litter cover (%)	11.2 ± 0.92	11.4 ± 0.99	0.2	215	0.84	11.4 ± 0.72	10.2 ± 1.91	0.5	215	0.60
Grass cover (%)	56.0 ± 1.26	50.7 ± 1.09	−3.2	215	0.002	53.6 ± 0.89	48.8 ± 2.47	1.6	215	0.11
Forb cover (%)	25.9 ± 1.36	27.1 ± 1.10	0.7	215	0.49	26.2 ± 0.89	29.2 ± 3.49	−1.0	215	0.33
Woody cover (%)	4.2 ± 0.78	5.1 ± 0.96	0.7[a]	210	0.51	4.4 ± 0.63	7.4 ± 2.95	−1.0[a]	19.7	0.19
Soil cover (%)	3.6 ± 0.45	5.7 ± 0.66	2.6[a]	194	0.009	4.7 ± 0.44	4.4 ± 1.25	0.2	215	0.85
Nest cover (%)	69.2 ± 2.79	64.8 ± 2.54	−1.2	217	0.23	66.2 ± 1.97	73.5 ± 6.34	−1.1	217	0.26
Nest height (cm)	18.7 ± 1.49	17.6 ± 1.49	−0.5	98	0.61	18.3 ± 1.15	17.6 ± 2.69	0.2	98	0.83

[a] t- and P-values for non-equal variance.

tion. In late June and throughout July, 18% of all nests were found in areas that had been burned the same spring and therefore lacked any litter. In these areas, Henslow's Sparrows placed their nests within large clumps of grass (mostly big bluestem and Indian grass) close to the ground. Successful and depredated Henslow's Sparrow nests did not differ in any nest characteristic (Table 5).

DISCUSSION

In southwestern Missouri, Dickcissels and Henslow's Sparrows had nearly identical clutch size, hatching success, length of incubation and nestling stages, and number of young fledged per successful nest. These variables were similar to previous reports for Dickcissels (Bent 1968, Harmeson 1974, Zimmerman 1982, Fretwell 1986, Patterson and Best 1996). Fewer studies have monitored Henslow's Sparrow nests, because their nests are difficult to locate (Bent 1968; Robins 1971; Schulenberg et al. 1994; D. Reinking, pers. comm.). Clutch size of Dickcissels and Henslow's Sparrows tended to decrease with date in the breeding season in southwestern Missouri. For Dickcissels, Harmeson (1974) described a peak in clutch size in the middle of the nesting season, whereas changes of Henslow's Sparrow clutch size over time had not yet been described.

Although Dickcissels and Henslow's Sparrows had almost identical nesting variables, their nesting phenologies seemed to differ. Generally, nesting success is relatively low in most grassland nesting birds, varying from 25–50% (Wiens 1969, Vickery et al. 1992, Martin 1995). Grassland birds often compensate for low nesting success by several renesting attempts throughout the breeding season. Consequently, most grassland nesting species raise an average of 1.5–2 broods per female per year (Wiens 1969, Martin 1995). The single nesting peak of Dickcissels in my study seemed to indicate that Dickcissels raised only one brood in my study area, as has been described by Zimmerman (1982, 1984). However, E. Bollinger (pers. comm.) observed a second brood in one color-banded Dickcissel female, indicating that Dickcissels can be double-brooded. Because Dickcissels appear to frequently move within one breeding season (Fretwell 1986), possibly because of displace-

TABLE 5. Henslow's Sparrow nest characteristics ($\bar{x} \pm$ SE) at successful and depredated nests in southwestern Missouri prairie fragments, 1995–1997.

Variable	Successful (n = 35)	Depredated (n = 25)	t	df	P
Litter depth (cm)	3.3 ± 0.37	3.7 ± 0.41	0.72	58	0.47
Vegetation height (cm)	43.0 ± 1.48	40.7 ± 1.71	−1.00	58	0.32
Visual obstruction (dm)	25.4 ± 1.89	24.9 ± 2.09	−0.20	57.7	0.84
No. woody stems	0.43 ± 0.14	0.26 ± 0.11	−0.94	57.7	0.35
Litter cover (%)	27.1 ± 2.70	33.1 ± 2.85	1.50	58	0.14
Grass cover (%)	51.4 ± 2.50	49.4 ± 2.43	−0.57	58	0.57
Forb cover (%)	19.1 ± 1.35	16.2 ± 1.58	−1.42	58	0.16
Woody cover (%)	1.82 ± 0.68	1.14 ± 0.45	−0.98	55.2	0.40
Soil cover (%)	0.55 ± 0.12	0.22 ± 0.11	−1.47	50.4	0.15
Nest cover (%)	89.6 ± 4.02	91.7 ± 3.03	0.41	57.7	0.68
Nest height (cm)	7.0 ± 0.63	7.9 ± 1.02	0.74	26.8	0.47

ment from hayfields after mowing (Igl 1991, Frawley and Best 1991), females might renest or raise a second brood in another area. None of the Dickcissels in my study area were color-banded; therefore, I could not determine if late nesting females (as also described by Harmeson 1974) had arrived from other areas, or if they had started a second brood or a renesting attempt in the same area.

Henslow's Sparrows seemed to be more likely to be double-brooded in southwestern Missouri than Dickcissels because they clearly exhibited two peaks of nest initiation. However, as with Dickcissels, individual birds were not color-banded, making it impossible to determine if the second nesting peak was caused by females on their second brood, by renesting attempts, by newly arriving females, or if it was an artifact of small sample size. This lack of adequate information is also true for all other studies that describe this species as double-brooded (Hyde 1939, Bent 1968, Robins 1971).

Nest predation was the main reason for nest failure, as has been described for many other bird species (Martin 1993, Patterson and Best 1996). Mean Mayfield nesting success of Dickcissels was similar to that reported from Kansas (Zimmerman 1984) and Missouri Crop Reserve Program fields (McCoy 1996), but lower rates of nesting success were reported from Iowa (Bryan and Best 1994, Patterson and Best 1996), Kansas (Hill 1976), and Oklahoma (Rohrbaugh et al. in press). Robins (1971) reported that 6 of 11 Henslow's Sparrow nests found in Michigan successfully fledged young. This apparent success rate (54.5%) is comparable to the apparent success rate in my study (57.6%). However, the number of young fledged per nest in Michigan (0.37) and the number of young fledged per successful nest (2.8) were lower than in Missouri. In Oklahoma, 40.9% of 22 Henslow's Sparrow nests were successful (D. Reinking, pers. comm.), which was about 17% lower than in Missouri. The number of young fledged per unparasitized Henslow's Sparrow nest was also slightly lower in Oklahoma than in Missouri (3.3 vs 3.6 young fledged per nest; Reinking, pers. comm.). Southwestern Missouri thus seems to be a relatively productive breeding area for Henslow's Sparrows.

Daily Mayfield nesting success in Dickcissels was lower during incubation than during nestling stages in 1996, and tended to be lower in 1995 and 1997. Higher nesting success during the nestling stage was also reported by Bryan and Best (1994) and by Harmeson (1974), and generally is the most frequently observed pattern of nest survival (Nice 1957; but see Patterson and Best 1996). Nesting success could be lower during incubation because poorly concealed nests are the first to be found by nest predators, or because visually hunting nest predators find nests with eggs more easily. Shorter and sparser vegetation at depredated Dickcissel nests indicated that these nests were in fact less well concealed than successful nests. High incidence of nest predation by mammals (see Winter 1998), which hunt based on visual and olfactory cues, might explain the tendency for slightly lower nesting success during incubation in southwestern Missouri. However, the only nest predators

that I observed at Dickcissel nests were two snakes, one eastern yellowbellied racer (*Coluber constrictor flaviventris*) and one prairie kingsnake (*Lampropeltis calligaster calligaster*). Because rates of nesting success in Henslow's Sparrows were nearly identical during incubation and nestling stages, and because their nests were extremely well concealed, it seems that visually hunting nest predators rarely destroy its nests. Instead of visually hunting predators, snakes are possibly the main nest predators of Henslow's Sparrow nests. This could also be the reason why nest vegetation did not differ between successful and depredated nests.

Rates of brood parasitism by Brown-headed Cowbirds in southwestern Missouri were relatively low compared to parasitism rates described in other studies on grassland-nesting birds (Hergenrader 1962; Zimmerman 1966, 1983; Hill 1976; Elliott 1978; Patterson and Best 1996; Koford et al. in press). Because cowbirds did not cause direct mortality to any Dickcissel young in my study, brood parasitism by itself did not directly decrease nesting success. However, the reduction in clutch size decreased the number of host fledglings by about one young per parasitized nest, as also was reported by Hill (1976).

In Henslow's Sparrows, brood parasitism by Brown-headed Cowbirds was slightly lower than in Dickcissels; only 5% of all Henslow's Sparrow nests were parasitized in southwestern Missouri. The only other records of parasitized Henslow's Sparrow nests are from Oklahoma (Reinking, pers. comm.) and Kansas (Schulenberg et al. 1994). In Oklahoma, 2 out of 22 Henslow's Sparrow nests were parasitized. Only 1 of the parasitized nests successfully fledged both host and cowbird young, whereas the other nest was depredated. The one Henslow's Sparrow nest that was found by Schulenberg and coauthors (1994) in Kansas contained two cowbird eggs and was abandoned during incubation. Cowbird parasitism is probably low in Henslow's Sparrows because their nests are well concealed. Low parasitism rates in Henslow's Sparrows were previously noted by Bent (1968:786), who mentioned that this species "appears to escape heavy parasitism, possibly because the nests are so well hidden."

Nest placement differed significantly between Dickcissels and Henslow's Sparrows. Dickcissels chose a variety of nesting habitats (Bent 1968); they preferred forbs and shrubs, and did not avoid edge habitats. Henslow's Sparrow nests, on the other hand, were never found in either of the nest substrates preferred by Dickcissels or within shrubby edge habitat. Instead, this species built its nest lower to the ground, mainly within large clumps of litter where it was almost 100% covered by vegetation (Hyde 1939, Robin 1971, Schulenberg et al. 1994). Several researchers that described the relationship between Henslow's Sparrow breeding densities and vegetation parameters also noted the species' preference for tall grass and litter cover (Wiens 1969, Skinner et al. 1984, Herkert 1994, Swanson 1996). I found that Henslow's Sparrows were able to build nests in recently burned areas that lacked litter, as did Zimmerman (pers. comm. in Schulenberg et al. 1994) in Kansas. Because Dickcissel nests were more conspicuous than Henslow's Sparrow nests, they were probably more easily detected by visually hunting nest predators and Brown-headed Cowbirds, resulting in slightly higher rates of nest predation and nest parasitism in this species.

General nesting data indicated that Dickcissels tended to be less productive in southwestern Missouri than Henslow's Sparrows. These findings are in contrast to the general notion that Dickcissels are of little conservation concern on the breeding grounds (Herkert et al. 1993, Swanson 1996). The discrepancy may be because previous reports on Dickcissels and Henslow's Sparrows were based only on breeding density estimates. This study showed that basic data on the general nesting ecology of a species are necessary for a better understanding of the factors that might influence a species in a given area.

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RESPONSE OF A BIRD ASSEMBLAGE IN SEMIARID CHILE TO THE 1997–1998 EL NIÑO

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ABSTRACT.—The semiarid region of Chile is influenced by El Niño Southern Oscillation. Its absence causes droughts and its presence causes wet years, which in turn result in variations in resource levels for avian assemblages. We show that bird species richness and density follow some of these pulses closely. Sixty-one bird species, 32 of which were Passeriformes, were sighted during five years in Las Chinchillas National Reserve (300 km N of Santiago). Overall, 30 species (49%) were residents and 31 (51%) were migratory. The most speciose trophic groups were insectivores (34%), carnivores (28%), and granivores (25%). Bird species richness and density declined from 43 species and 45–50 individuals/ha in spring 1993, to 29 species and 15–20 individuals/ha in autumn 1996. Increases were observed with the onset of El Niño, reaching totals of 42 species (a 45% increase from 29) and densities of 55–60 birds/ha in summer 1997. Similar trends were observed in one of two major food resources measured: small mammals. Positive correlations were found between raptor species richness and density and small mammal density, but not between insectivorous bird species richness or density and terrestrial arthropod abundance. Because the climate was very dry during most of the time of our study, we may have witnessed the lowest boundary for species richness and bird density. Whether the 1997–1998 El Niño brought the maximum bird species richness and density for the site is yet to be seen. *Received 20 Jan. 1999, accepted 2 June 1999.*

Bird assemblages vary through time in species composition and absolute and relative abundances, in the short term (seasonal, Avery and van Riper 1989), medium term (between years, Wiens 1990a, b), or both. Most authors agree that this variation reflects changes in the resource base, mainly food (Feinsinger et al. 1985, Wiens 1993). Three factors are generally proposed to account for how birds use resources (Pearson 1991): competition (Martin 1987, Pulliam and Dunning 1987), predation (Lima 1987), and physical or abiotic stresses (Karr and Freemark 1983). The degree to which these factors determine bird assemblages is controversial (Loiselle and Blake 1991). Although they are not mutually exclusive, these three factors are usually assessed individually, rarely two simultaneously (Martin 1985, Kotler and Holt 1989). Most attention has concentrated on the role of species interactions rather than on physical factors (Pearson 1991), although arguably the latter set the stage for biotic interactions.

The periodic intrusion of El Niño Southern Oscillation along the western coasts of the Americas constitutes a major physical disturbance that brings warm water to the shores and increased precipitation to the adjacent land masses. Although initially studied in its oceanographic and climatic aspects, increased awareness of the multiple effects of El Niño is shifting the focus to the effects of this phenomenon on birds (Barber and Chavez 1983, Schreiber and Schreiber 1984, Gibbs and Grant 1987, Grant and Grant 1987, Hall et al. 1988, Miskelly 1990, Massey et al. 1992, Lindsey et al. 1997). Previous studies dealt with the putative El Niño effects on seabird colonies or on terrestrial island birds. Effects on inland birds have been little studied.

The semiarid areas of northcentral Chile (27–32° S), apart from seasonal fluctuations in weather and food resources, are characterized by medium term fluctuations in rainfall (Fuentes et al. 1988). Accordingly, plant cover, amount of herbage production, and size of seed bank vary markedly among years (Gutiérrez et al. 1993). Small mammals track these food resources closely (Jiménez et al. 1992) and perhaps arthropods do also (Fuentes and Campusano 1985). It has become increasingly clear that the unusual rainfall brought by El Niño events to semiarid Chile are responsible for increased primary productivity, which in turn leads to population outbreaks of small mammals and to local increases in the populations of carnivorous birds that prey on them (Meserve et al. 1995; Jaksic et al. 1996, 1997).

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Interestingly, no multi-year studies have been conducted on the response of an entire bird assemblage in such semiarid areas to changes in precipitation, or in primary (vegetation) or secondary production (mammals, arthropods). Here we report upon the effect of variation in such secondary production on bird species richness and density.

STUDY AREA AND METHODS

Study area.—The study site is located inside Las Chinchillas National Reserve (simply called the reserve hereafter), at 31° 30′ S, 71° 06′ W, about 300 km N of Santiago, Chile, and 60 km E of the Pacific coast. The reserve spans 400–1700 m elevation, has a rugged topography, and is dominated physiographically by an alternation of ridges and ravines, with few flat areas between. The climate is classified as semiarid by di Castri and Hajek (1976), with sporadic precipitation concentrated during Austral winter months (June through August). Mean annual rainfall 1986–1997 was 170 mm, but with marked increases in 1987 (513 mm), 1992 (307 mm), and 1997 (367 mm) associated with the respective El Niño events (1986–1987, 1991–1992, 1997–1998). Two dominant landscape types characterize the study site: ravines and slopes. Ravines are more vegetated (70.3% shrub cover) than slopes (52.7% cover).

Vegetation.—The vegetation is a thornscrub composed mainly of spiny dicots, bromeliads, and cacti (details in Gajardo 1978). Dominant species in ravines are *Stevia* sp. (15.5% cover), *Colliguaya odorifera* (12.5%), *Pleocarphus revolutus* (6.6%), *Baccharis paniculata* (5.4%), *Proustia cuneifolia* (5.4%), and *Maytenus boaria* (5.2%). Dominant species in slopes are *Bahia ambrosioides* (16.9%), *Proustia cuneifolia* (19.3%), *Baccharis paniculata* (8.6%), *Porlieria chilensis* (8.0%), *Lobelia polyphylla* (4.0%), and *Puya berteroniana* (3.0%).

Census techniques.—During the four calendar seasons of every year from July (winter) 1993 to January 1998 (summer), we conducted fixed band transects to census birds (Burnham et al. 1980, Conner and Dickson 1980, Bibby et al. 1993). One transect was in a ravine (1500 × 20 m = 3 ha, time spent = 45–55 min/transect) and another in a southern exposure mid-slope (500 × 40 m = 2 ha, 20–30 min/transect) of each El Cobre and El Grillo creek beds (sampling effort = 4 transects/season, the two creek beds combined). The two ravine transects were surveyed throughout the study period, but the two on slopes were terminated in the summer of 1995. The two creek beds were dry except for the wet winter of 1997, but are hereafter called creeks nonetheless. Transects were started 1 h after the sun's rising above the top of ridges east of the two creeks. Diurnal raptors (Falconiformes) were censused opportunistically in a 2000 ha area centered around the two creeks. The abundance of the four nocturnal raptor species (Strigiformes) at the site was assessed based on responses to playbacks of their calls (Johnson et al. 1981, Haug and Didiuk 1993) 0.5 h after the first star was spotted in the sky. Every playback was broadcast for 1 min for each species sequentially, at four fixed stations located in the ravine of the El Cobre creek, at two stations in the ravine of El Grillo creek, and at two stations in the bottom of the cliffs that border the Aucó stream. For the Strigiformes, we considered the area sampled to be about 2000 ha, and all estimates of abundance refer to the minimum number of individuals detected. All densities are standardized as the number of individuals per species per hectare.

Bird categorizations.—Bird nomenclature follows Meyer de Schauensee (1982). We categorized species according to their reproductive status, diet, residence status, and habitat. Reproduction: birds were classified as either nesting or non-nesting at the site, depending on whether they were observed actually nesting. Some cryptic nesters may have escaped our detection and thus the number of nesting species may be underestimated. Diet: we followed Jaksic and Feinsinger (1991) in establishing the following primary diets: carnivores, insectivores, granivores, nectarivores, frugivores, folivores, and omnivores. These categorizations come from the literature or from direct observation. Residence: we considered a species to be resident at the study site if it was observed on 13 (ca 70%) of the 19 visits to the site. A species was categorized as migrant, either if it stayed at the site only during spring and summer (summer visitor) or if it stayed only during autumn and winter (winter visitor). Habitat: the following landscape units were considered as "habitats": ravines (bottom of creeks), slopes (sides of creeks), flat areas, and water edges (around permanent streams).

Food availability.—Small mammal density was assessed during five days/four nights trapping bouts in each season on opposite slopes of El Cobre creek. Each of the two grids consisted of a 7 × 7 arrangement of stations at 15 m intervals equipped with one Sherman live trap at each station. Total trapping area was 2.2 ha. Jiménez and coworkers (1992) provided details of this trapping scheme. Terrestrial arthropods were sampled with Barber pitfall traps (Southwood 1978) consisting of a 200 ml plastic vial with its rim at ground level, inside of which a 100 ml plastic vial was tightly fitted and filled with water and biodegradable detergent. One hundred such traps were placed at El Cobre creek along four transects with stations at 10 m intervals. Two transects were on opposite slopes and had 20 traps each; two transects (with 30 traps per transect) were in the ravine. Specimens were collected at 24 h intervals during two consecutive days and their total abundance expressed as individuals per trap per 24 h. This total abundance was weighted by the proportion of traps placed in each habitat type (2:3, slopes:ravine). Unlike the case for mammals, this method provides information only on relative densities of large terrestrial arthropods through time.

Statistical analyses.—To determine whether there were associations between habitat and bird densities through time, we compared data obtained in the two

slopes with those from the two ravines because these were the two physiognomically most salient landscape features in the reserve. The degree of association between bird densities and two food resources (mammals and arthropods) was determined separately for carnivorous (Falconiformes and Strigiformes) and insectivorous birds by Spearman correlation coefficients (Sokal and Rohlf 1981). Because raptor sightings could not be assigned unequivocally to either slopes or ravines (as they apparently hunted in both habitat types), these data were pooled. In the case of insectivorous birds, we could assign sightings unequivocally to one or the other of the two habitats, and thus we were able to make separate comparisons with arthropod abundance in either slopes or ravines. Bird and arthropod densities were compared by means of Wilcoxon matched-pairs tests (Sokal and Rohlf 1981). The results from Barber traps may be considered only as approximations of terrestrial arthropod density. We did not sample aerial or foliage arthropods. All statistical analyses were performed with software Systat version 7.0 for Windows 95.

RESULTS

Characterization of the bird assemblage.—We sighted 61 species during our 5 year study (Table 1), 32 (53%) of which were Passeriformes. Thirty species (49%) were residents (but only 13 species were sighted in all 19 visits). Transient species were equally divided between winter visitors (10%) and summer visitors (10%). Another 31% of the species were sighted too few times to enable us to categorize them, save as accidentals or occasionals. Two species were not observed but known to be present. The White-tailed Kite (*Elanus leucurus*) had been sighted previously (Jaksic et al. 1996) and thus we categorized it as a migrant. We considered the Great Horned Owl *Bubo virginianus* to be resident, despite having detected it during only five visits because we collected freshly regurgitated pellets at each visit (Jaksic et al. 1996).

In terms of species numbers, the best represented trophic groups were insectivores (34%), carnivores (28%), and granivores (25%), accounting for 87% (53 species) of the local assemblage (Table 1). Thirty-eight (62%) of the 61 species nested in the reserve, including three summer visitors: Aplomado Falcon (*Falco femoralis*), Giant Hummingbird (*Patagona gigas*), and White-tufted Tyrant (*Elaenia albiceps*; Table 1). Seventy-seven percent of the species were sighted in ravines, 54% on slopes, 11% on flat areas, and 7% near small streams and ponds. (These percentages add to more than 100% because some species visit more than one habitat type; Table 1.) Bird densities were not different, either between the two ravines (Wilcoxon matched-pairs test; $Z = 0.283$; $n = 19$; $P > 0.05$) or between the two slopes ($Z = 0.891$; $n = 11$; $P > 0.05$). Thus, we felt justified to analyze our data from the two creeks by habitat type only.

Multi-year trends.—Drought conditions prevailed during the first four years of our study (1993–1996); rainfall ranged 40–106 mm compared to a mean of 170 mm for 1986–1997 (Fig. 1). By contrast, 1997 had over twice the mean annual precipitation recorded for the study site (Fig. 1). Concomitantly, there was a declining trend in bird species richness from 43 species in winter 1993 to 29 at the end of the drought in autumn 1997 (a 33% decrease; Fig. 1). Twenty-nine species may well represent the minimum number of bird species present in the reserve at any time. As soon as El Niño driven precipitation reappeared at the site (the previous two occurrences were 1987 and 1992), there was an increase from 29 species in autumn 1997 to 42 species in summer 1997 (a 45% increase; Fig. 1). Whether this is close to the maximum bird species richness that the site can accommodate has not been determined.

Bird density also tracked precipitation patterns (Fig. 2). Bird numbers in ravines declined from about 45–50 individuals/ha (1993) to about 10/ha in summer 1994 (the driest year in the series; Fig. 1), and started a slow recovery through 1995 and 1996, reaching densities of 55–60 birds/ha during summer 1997. Bird densities on slopes were apparently less than those in ravines (Fig. 2) but paralleled the same trends until summer 1995, when we terminated censuses on slopes.

Similar trends were observed among small mammals but not among terrestrial arthropods (Fig. 3). Small mammals declined markedly through 1993 and 1994, remained at very low levels 1995–1996, and recovered after the spring 1997 (Fig. 3). Terrestrial arthropods did not display such marked fluctuation (Fig. 3). There were significant positive correlations between small mammal density and both raptor species richness ($r_s = 0.77$, df = 17, $P < 0.001$) and raptor density ($r_s = 0.76$, df = 17, $P < 0.001$). Although positive, there were no

TABLE 1. Birds of Las Chinchillas National Reserve (northeentral Chile) and their categorization by reproductive status, dietary category, residence status (in parentheses, number of calendar seasons the species was sighted), and habitat type (landscape aspect).

Species	Reproduction	Diet	Residence	Habitat
Nothoprocta perdicaria	Nesting	Granivore	Resident (18)	Ravine/Slope
Casmerodius albus	Non-nesting	Carnivore	Migrant (6)[a]	Water edge
Egretta thula	Nesting	Carnivore	Migrant (8)	Water edge
Nycticorax nycticorax	Non-nesting	Carnivore	Migrant (1)	Water edge
Vultur gryphus	Non-nesting	Carnivore	Migrant (5)	Slope
Elanus leucurus	Non-nesting	Carnivore	Migrant (0)[b]	Flat areas
Geranoaetus melanoleucus	Nesting	Carnivore	Resident (16)	Ravine/Slope
Buteo polyosoma	Nesting	Carnivore	Resident (14)	Ravine
Parabuteo unicinctus	Non-nesting	Carnivore	Migrant (8)	Flat areas
Milvago chimango	Nesting	Insectivore	Resident (14)	Ravine/Flat areas
Falco peregrinus	Non-nesting	Carnivore	Summer visitor (5)	Ravine/Slope
Falco femoralis	Nesting	Carnivore	Summer visitor (4)	Slope
Falco sparverius	Nesting	Insectivore	Resident (13)	Ravine/Flat areas
Callipepla californica	Nesting	Granivore	Resident (19)	Ravine/Slope
Rallus sanguinolentus	Nesting	Carnivore	Migrant (8)	Water edge
Vanellus chilensis	Nesting	Carnivore	Resident (14)	Flat areas
Columba araucana	Non-nesting	Granivore	Winter visitor (3)	Ravine
Zenaida auriculata	Nesting	Granivore	Resident (14)	Ravine/Slope
Metriopelia melanoptera	Unknown	Granivore	Summer visitor (11)	Ravine/Slope
Cyanoliseus patagonus	Unknown	Frugivore	Resident (15)	Ravine
Tyto alba	Nesting	Carnivore	Migrant (11)	Ravine/Slope
Bubo virginianus	Nesting	Carnivore	Resident (6)[b]	Ravine/Slope
Glaucidium nanum	Nesting	Carnivore	Resident (13)	Ravine/Slope
Speotyto cunicularia	Nesting	Carnivore	Resident (16)	Ravine/Slope
Caprimulgus longirostris	Nesting	Insectivore	Resident (19)	Ravine
Patagona gigas	Nesting	Nectarivore	Summer visitor (12)	Ravine/Slope
Sephanoides galeritus	Non-nesting	Nectarivore	Winter visitor (10)	Ravine/Slope
Colaptes pitius	Non-nesting	Insectivore	Migrant (8)	Slope
Picoides lignarius	Nesting	Insectivore	Resident (19)	Ravine/Slope
Geositta rufipennis	Non-nesting	Granivore	Winter visitor (6)	Ravine/Slope
Upucerthia dumetaria	Non-nesting	Insectivore	Migrant (10)	Ravine
Upucerthia ruficauda	Non-nesting	Insectivore	Summer visitor (5)	Ravine
Chilia melanura	Nesting	Insectivore	Resident (19)	Ravine/Slope
Leptasthenura aegithaloides	Nesting	Insectivore	Resident (19)	Ravine/Slope
Asthenes modesta	Nesting	Insectivore	Resident (16)	Ravine/Slope
Pteroptochos megapodius	Nesting	Insectivore	Resident (19)	Ravine/Slope
Scelorchilus albicollis	Nesting	Insectivore	Resident (19)	Ravine/Slope
Scytalopus magellanicus	Nesting	Insectivore	Resident (16)	Ravine
Agriornis livida	Non-nesting	Carnivore	Migrant (7)	Slope
Pyrope pyrope	Nesting	Insectivore	Resident (18)	Ravine/Slope
Muscisaxicola macloviana	Non-nesting	Insectivore	Winter visitor (2)	Ravine/Slope
Elaenia albiceps	Nesting	Insectivore	Summer visitor (7)	Ravine
Anairetes parulus	Nesting	Insectivore	Resident (18)	Ravine/Slope
Colorhamphus parvirostris	Non-nesting	Insectivore	Winter visitor (8)	Ravine
Tachycineta leucopyga	Nesting	Insectivore	Resident (19)	Flat areas
Pygochelidon cyanoleuca	Non-nesting	Insectivore	Migrant (3)	Flat areas
Troglodytes aedon	Nesting	Insectivore	Resident (19)	Ravine/Slope
Phytotoma rara	Non-nesting	Folivore	Migrant (1)	Ravine
Turdus falcklandii	Nesting	Omnivore	Migrant (9)	Ravine
Mimus thenca	Nesting	Omnivore	Resident (19)	Ravine/Slope
Sicalis sp.	Non-nesting	Granivore	Migrant (3)	Ravine
Zonotrichia capensis	Nesting	Granivore	Resident (19)	Ravine/Slope
Sturnella loyca	Nesting	Omnivore	Resident (19)	Ravine
Curaeus curaeus	Nesting	Omnivore	Resident (16)	Ravine/Slope
Phrygilus gayi	Non-nesting	Granivore	Winter visitor (8)	Ravine/Slope

TABLE 1. CONTINUED.

Species	Reproduction	Diet	Residence	Habitat
Plurygilus fruticeti	Nesting	Granivore	Resident (18)	Ravine/Slope
Plurygilus alaudinus	Nesting	Granivore	Migrant (8)	Ravine
Diuca diuca	Nesting	Granivore	Resident (19)	Ravine/Slope
Carduelis uropygialis	Non-nesting	Granivore	Migrant (2)	Ravine
Carduelis barbatus	Non-nesting	Granivore	Migrant (2)	Slope
Passer domesticus	Nesting	Granivore	Migrant (12)	Ravine

[a] Species categorized simply as migrants did not yield enough data to determine whether they are summer or winter visitors, occasionals, or accidentals.
[b] Not sighted during our work, but present in the area. See text for details.

significant correlations between terrestrial arthropod abundance and insectivorous bird species richness (r_s = 0.06, df = 17, $P > 0.05$), density on slopes (r_s = 0.49, df = 9, $P > 0.05$) nor density on ravines (r_s = 0.37, df = 17, $P > 0.05$).

During the transition from drought (1993–1996) to wet year (1997), two previously unrecorded species arrived at the reserve, the folivorous Rufous-tailed Plantcutter (*Phytotoma rara*) and the fish and amphibian eating Brown Heron (*Nycticorax nycticorax*).

DISCUSSION

The percentage (51%) of species at our study site that were migrants, is similar (48% of 88 species) to that reported by Marone (1992a,b) in the Monte scrubland across the Andes at similar latitudes in Argentina. As in Chile, the high percentage of migrants in the

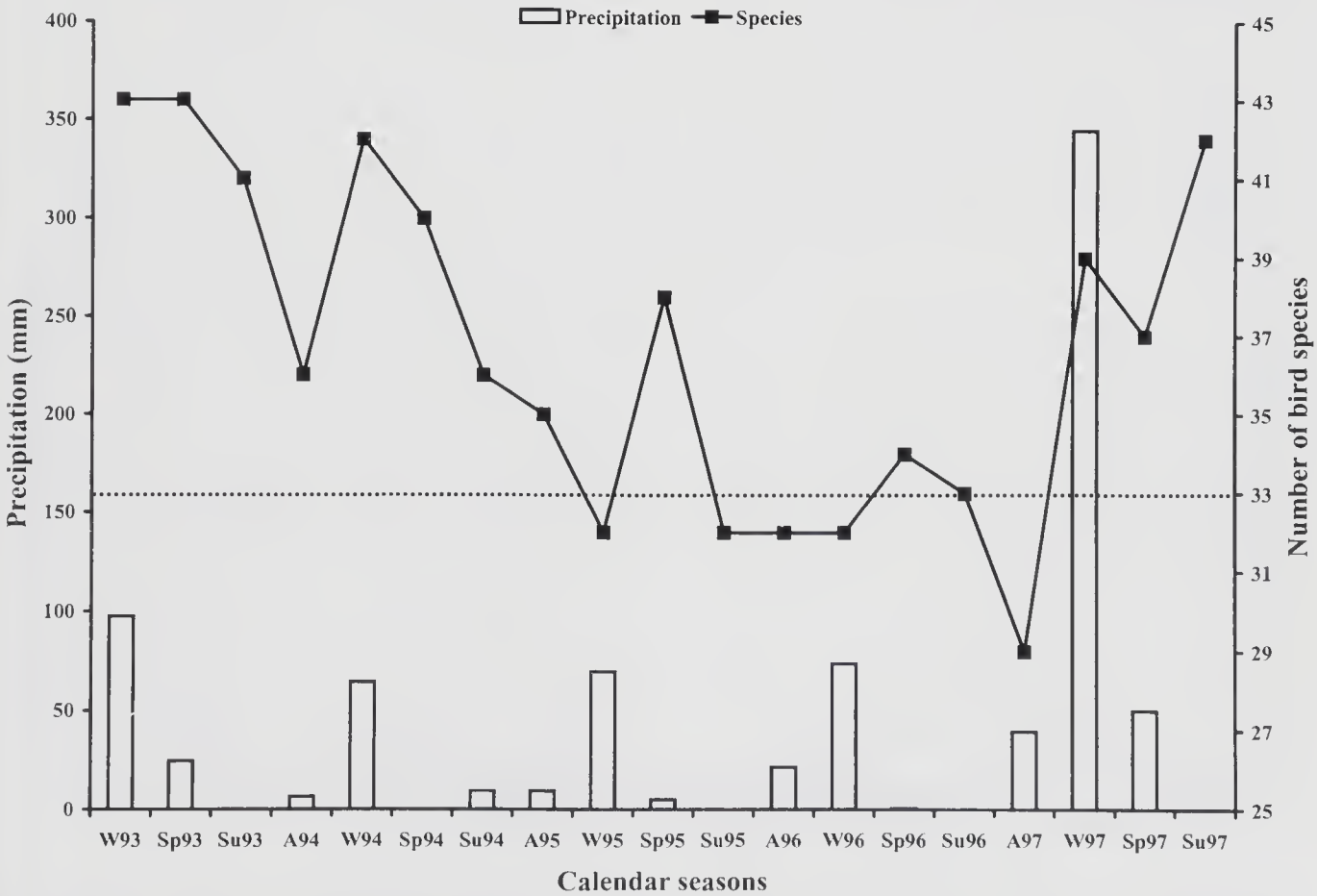

FIG. 1. Seasonal variation in rainfall and number of bird species at Las Chinchillas National Reserve throughout the study period (19 calendar seasons = 5 years). W = Winter (June–August), Sp = Spring (September–November), Su = Summer (December–February), A = Autumn (March–May). The segmented line represents the mean annual rainfall of the last 12 years.

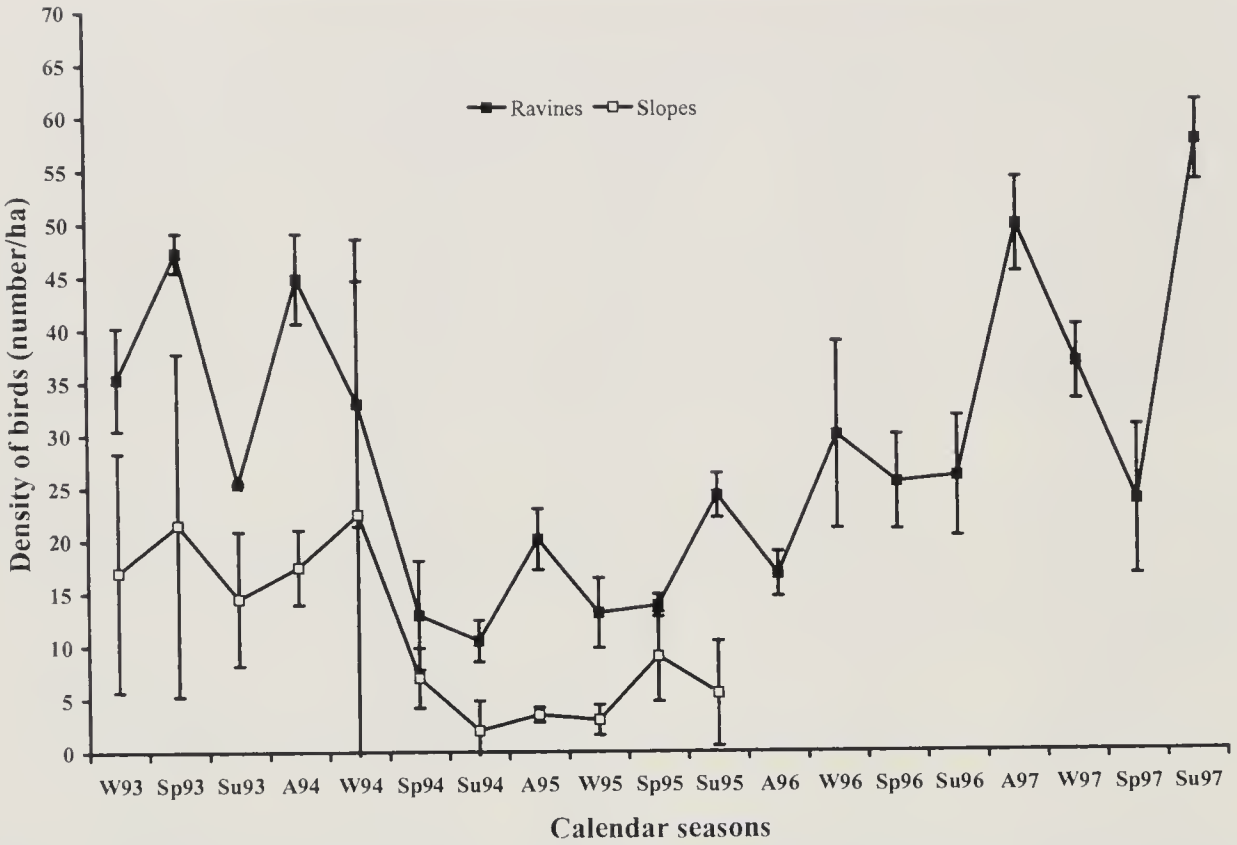

FIG. 2. Bird density (mean ± SD) at the reserve throughout the study period, by habitat type: ravines and slopes. W = Winter, Sp = Spring, Su = Summer, A = Autumn. Censuses on the slopes were discontinued after summer 1995.

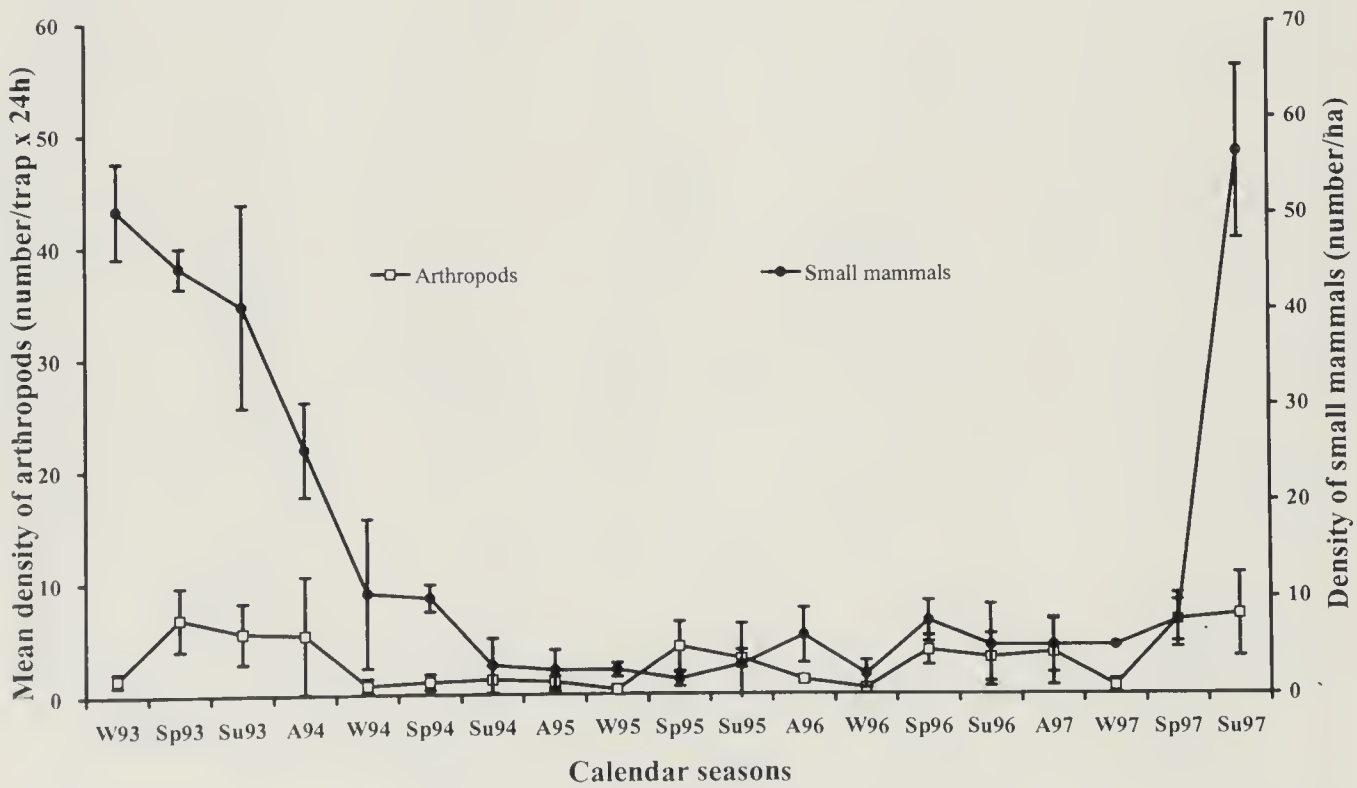

FIG. 3. Abundance of terrestrial arthropods (mean ± SD) and of small mammals (mean ± SD) at the reserve throughout the study period. Abundance of arthropods is the mean of four samples (two from opposite facing slopes and two from a ravine), that of mammals is an average for the north and south facing slopes. W = Winter, Sp = Spring, Su = Summer, A = Autumn.

Argentine Monte may be associated with the extreme fluctuations in precipitation that characterize arid and semiarid regions of South America. Varying precipitation levels in Chile are associated with changes in primary and secondary production (Fuentes and Campusano 1985; Jaksic et al. 1996, 1997). Migrant birds may exploit these unpredictable resources by moving north from the more mesic Mediterranean region of central Chile or down from the Coastal Range to the west or the Andes to the east of our study area.

Marone (1992a,b) observed that insectivores (52%), carnivores (19%), and granivores (15%) dominated the Argentine Monte, accounting for 86% of the local assemblage, similar to the 87% we recorded in Chile. Nevertheless, there were more insectivores and fewer carnivores and granivores in the Argentine site than in our Chilean site. This suggests that there may be differences in resource levels between Chilean and Argentine semiarid sites. More data are needed from the Monte.

We detected positive correlations between number and/or density of bird species and specific resource levels (i.e., with regard to small mammals but not to terrestrial arthropods). Gutiérrez and coworkers (pers. comm.) measured the seed bank of the reserve before (1996) and during El Niño (1997). We found a positive association between this resource and richness/density of granivorous birds during the respective years. In central Chile, López-Calleja (1995) found that the granivorous Diuca Finch (*Diuca diuca*) and Rufous-collared Sparrow (*Zonotrichia capensis*), two species that were also present at our site, changed their seed preferences in response to short-term fluctuations in seed abundance. A detailed study of the abundance of these two species and their respective diets in relation to the seed bank in the reserve is needed.

Why were birds in our study site more abundant in ravines than in slopes? Perhaps food levels are higher in ravines than on slopes. Also, there is more vegetated ground in ravines (70%) than on slopes (53%). Structural aspects of the former habitat may render it more attractive to birds. The presence of a tree layer (e.g., *Maytenus boaria, Quillaja saponaria*) in ravines, which is absent from slopes, may favor higher bird densities because it provides more shelter, roosting and nesting sites, and perhaps greater food diversity (e.g., foliage insects).

The bird assemblage in the reserve showed both short (seasonal) and multi-year variation in its composition and density. Although bird species richness and density in our study site were lower during drought years and higher during wet years, it should be noted that droughts are more frequent and last longer than El Niño events (eight dry years versus four wet ones in 1986–1997). In a semiarid climate, perhaps dry years set the baseline in species richness and density for the bird assemblage, and both increase during wet years because of the immigration of opportunistic species from elsewhere. Thus, El Niño driven rains impose a strong abiotic influence, which cascades from increased primary and secondary productivity to bird species richness and density.

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POTENTIAL FOR PREDATOR LEARNING OF ARTIFICIAL ARBOREAL NEST LOCATIONS

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ABSTRACT.—We examined the potential for predators to learn the location of artificial arboreal (1.5 m above ground) nests in a managed forested landscape of central Pennsylvania from June–July 1995. We tested the hypothesis that predators do not learn the location of artificial arboreal nests placed repeatedly at the same sites (fixed nests) versus those placed at random sites in three habitats created by clearcutting (forested patches, forested corridors, contiguous forest). Sixty-nine (23%) of 299 total nests in five combined trials were disturbed by predators; 11 (16%) of these disturbances were attributed to corvids. Predation rates were greater on nests placed at random (28%) compared to fixed sites (18%, $P < 0.05$), indicating predators did not learn or return to the location of arboreal nests during our study. Predation rates varied significantly ($P < 0.001$) among habitats, with 49% of the nests disturbed in the forested-patch habitat versus only 7% and 13% in forested-corridor and contiguous-forest habitats, respectively. We propose that predation was higher in forested patches than in the other two habitats because the former had greater amounts of edge. *Received 12 Nov. 1998, accepted 10 May 1999.*

Artificial nest studies have been useful in examining the relationships between avian nesting success and landscape patterns (e.g., Paton 1994, Bayne and Hobson 1997). Several investigators have indicated that depredation of artificial and natural avian nests in managed forests varies with landscape patterns created by clearcutting (Yahner and Ross 1995, Vander Haegen and DeGraaf 1996, Yahner and Mahan 1996a). However, if predation rates on artificial nests are used as an indicator of temporal or spatial trends in avian nesting success (Yahner 1996, Sargent et al. 1998, Wilson et al. 1998), then the potential effect of the ability of predators to learn the locations of artificial nests needs to be determined. For example, as a consequence of clearcutting in a localized area, the availability of suitable nest sites may decline, thereby enabling predators to find nests located in the remaining uncut forested tracts (patches or corridors).

Forest clearcutting for Ruffed Grouse (*Bonasa umbellus*) at the Barrens Grouse Habitat Management Area (GHMA) in central Pennsylvania provided us with an ideal opportunity to test the hypothesis that predation rates did not vary between artificial arboreal (1.5 m above ground) nests placed at sites used repeatedly (fixed nests) versus random sites in a managed forested landscape. To our knowledge, predation rates on artificial nests at fixed vs random sites has been examined only with ground nests (Yahner and Mahan 1996a).

STUDY AREA AND METHODS

Our study was conducted on a 1166-ha Barrens GHMA, State Game Lands 176, Centre County, Pennsylvania, where a series of experimental studies dealing with depredation of artificial and actual nests have been conducted (e.g., Yahner and Wright 1985, Yahner 1991, Yahner and Ross 1995, Yahner and Mahan 1996a). The Barrens GHMA includes reference (contiguous forest habitat) and treated (forested-patch and forested-corridor habitats) sectors of similar size (Fig. 1). The treated sector is divided into 136 contiguous 4-ha blocks, and each block is partitioned into four 1 ha (100 × 100 m) plots arranged in a clockwise pattern (plots A–D). At the first cutting cycle (winter 1976–1977), plot A was clearcut in each block. At the second cycle (winter 1980–1981), plot B was clearcut in each block of the forested-patch habitat. At the third and last cycle (winters 1985–1986 and 1986–1987), plot B in each block of the forested-corridor habitat and plot C in each block of the forested-patch habitat were clearcut. The remaining uncut plots in the treated sector and forest in the reference sector have not been clearcut for 75–80 years. As a result of these three cutting cycles, a mosaic of uncut plots (plot D) entirely surrounded by clearcut plots of three age classes (plots A–C) occurred in the forested-patch habitat, whereas 100 m wide corridors of uncut plots (plots C–D) remained in the forested-corridor habitat (Fig. 1).

We placed artificial arboreal (1.5 m above ground) nests during five time periods (trials) from early June through July 1995 (Yahner and Mahan 1996a). A trial was 6 days in length, with 8 days between trials. At

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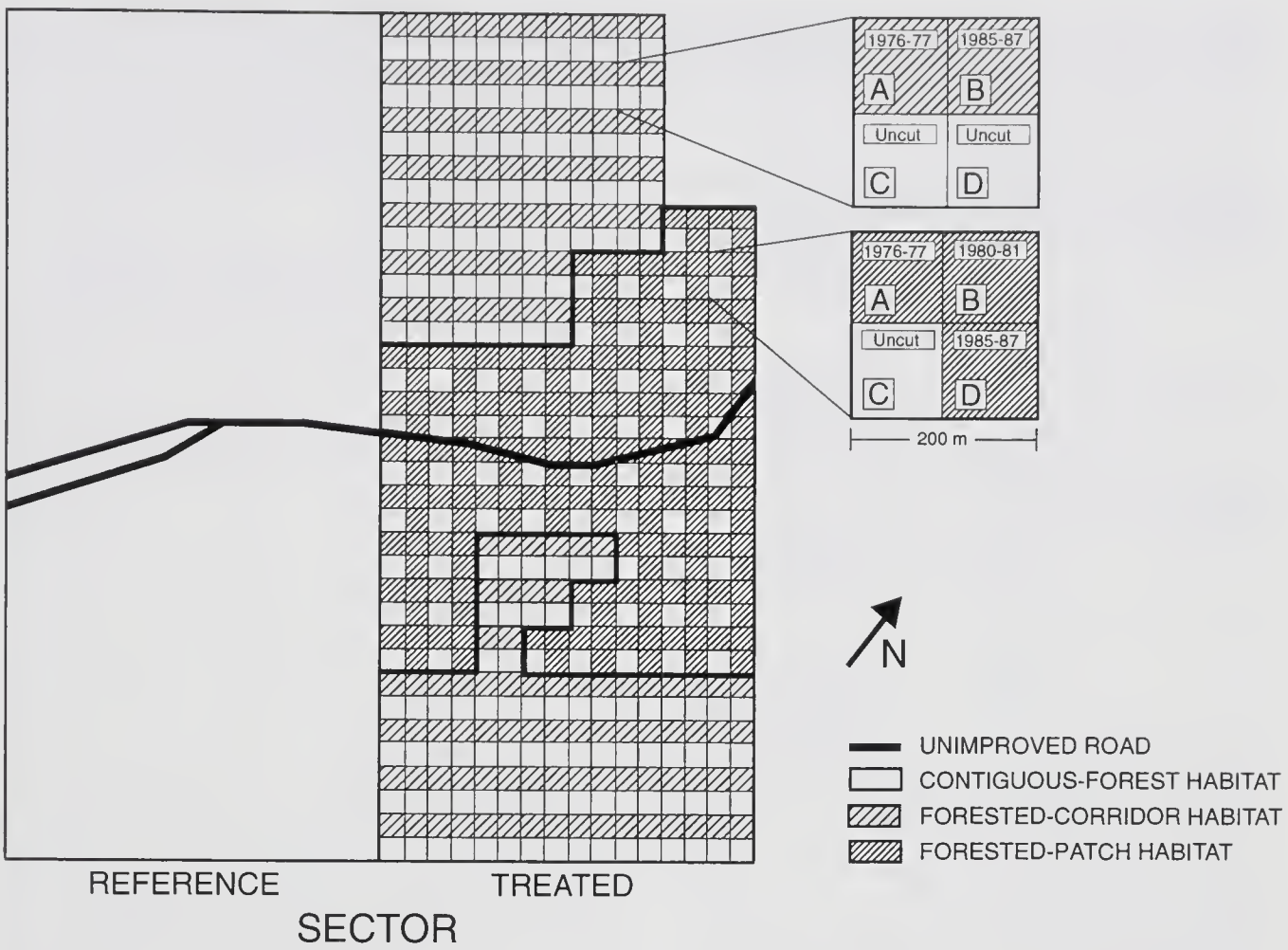

FIG. 1. Schematic of reference and treated sectors at the Barrens GHMA, Centre County, Pennsylvania. Dates of cutting cycles are given in plots A and B of the 76 blocks in the forested-corridor habitat of forest clearcutting and in plots A–C of the 60 blocks in the forested-patch habitat of clearcutting. Forest in the contiguous-forested habitat of clearcutting (reference sector), in plots C and D of the forested-corridor habitat, and in plot D of the forested-patch habitat.

the beginning of the study, 10 uncut plots (plot D) were chosen randomly in both forested-patch and forested-corridor habitats and 10 sites were randomly selected in the contiguous forest. These 30 sites were designated as fixed nests and were used in all trials (1–5) for nest placement. For each trial, we randomly chose 10 additional uncut plots (plot D) each in both forested-patch and forested-corridor habitats and 10 sites in the contiguous forest; these additional 30 sites were termed random nests. This resulted in 60 nests/trial, with 20 nests/habitat (forested patch, forested corridor, and contiguous forest) and 30 nests/nest-site type (fixed and random).

Artificial nests (10 cm diam and 10 cm deep) were constructed of chicken wire painted flat black to reduce glare and lined with leaf litter; nests were attached to the nearest woody stem (1–5 cm dbh) with green wire (Yahner and Scott 1988). Two fresh, brown chicken eggs were placed in each nest and sunk slightly below the rim of the nest to minimize detection. We chose large brown chicken eggs in this study because they allowed us to directly compare our results with those obtained in other studies at the study site, including artificial ground and arboreal nest studies conducted before the third cutting cycle (e.g., Yahner and Wright 1985, Yahner and Scott 1988), an artificial ground nest study conducted after the third cutting cycle (Yahner and Mahan 1996a), and a study of Wood Thrush nesting success after the third cutting cycle (Yahner and Ross 1995). One nest was established at each site. In forested-patch and forested-corridor habitats, nests were located 50 m from an edge in the center of plot D; in the contiguous forest, nests were placed at least 50 m from an edge (e.g., logging road). Rubber gloves and boots were worn when placing nests to reduce human scent (Nol and Brooks 1982).

We determined the fates of nests (e.g., undisturbed, disturbed by an avian predator, disturbed by a nonavian predator) at the end of each trial (Yahner and Mahan 1996a). Nest predators were classified by mode of disturbance and general nest appearance; eggs with peck holes were categorized as preyed upon by birds, and nests without eggs or with crushed eggs were classified as preyed upon by nonavian predators (Rearden 1951, Yahner and Scott 1988, Hernandez et al. 1997). Eggs and egg fragments were removed from nests at

TABLE 1. Fate of artificial arboreal nests in relation to type of nest site, habitat, and trial in a managed forested landscape at the Barrens GHMA, Centre County, Pennsylvania, June–July 1995.

Nest fate	Type of nest-site	Habitat	Trial					
			1	2	3	4	5	Total
Undisturbed	Fixed	Forested patch	8	7	5	4	6	30
		Forested corridor	8	9	8	10	10	45
		Contiguous forest	9	9	9	10	10	47
			25	25	22	24	26	122
	Random	Forested patch	7	3	4	3	4	21
		Forested corridor	10	10	8	10	9	47
		Contiguous forest	7	9	6	10	8	40
			24	22	18	23	21	108
Disturbed	Fixed	Forested patch	2	3	5	6	4	20
		Forested corridor	1	1	2	0	0	4
		Contiguous forest	1	1	1	0	0	3
			4	5	8	6	4	27
	Random	Forested patch	3	7	6	7	6	29
		Forested corridor	0	0	2	0	1	3
		Contiguous forest	3	1	4	0	2	10
			6	8	12	7	9	42

the end of each trial. The location of one nest in the forested-corridor habitat was not found after nest placement during trial 1.

Common bird species nesting in uncut forest within 2 m of ground level at the Barrens Grouse HMA were Wood Thrush (*Hylocichla mustelina*) and Eastern Towhee (*Pipilo erythrophthalmus*; Yahner 1991). Potential predators on artificial arboreal nests were American Crow (*Corvus brachyrhynchos*), Blue Jay (*Cyanocitta cristata*), and raccoon (*Procyon lotor*; Yahner and Scott 1988, Yahner and Morrell 1991). Smaller mammalian predators, e.g., eastern chipmunk (*Tamias striatus*) and white-footed mice (*Peromyscus leucopus*), probably had minimal effect on our artificial nests because of the relatively large egg size (see Roper 1992, Haskell 1995, DeGraaf and Maier 1996, Yahner and Mahan 1996b).

We examined dependency of nest fate (undisturbed and disturbed) on nest-site type (fixed versus random), habitat (forested patch, forested corridor, and contiguous forest), and trial (1–5) using a four-way test-of-independence (BMDP4F, Log-Linear Model; Dixon 1990). Likelihood ratios (G^2) were used to determine interactions of nest fate with the three other variables using log-linear models (Dixon 1990, Sokal and Rohlf 1995). If nest fate was dependent on a variable with more than two levels, we used 2 × 2 G-tests-of-independence about the cell(s) of interest.

RESULTS

Sixty-nine (23%) of the 299 artificial arboreal nests were disturbed during the five trials combined (Table 1); one nest location was not found in trial 1. We attributed 11 (16%) of the disturbed nests to avian predators. Nest fate was dependent on nest type, with fewer arboreal nests disturbed at fixed than at random sites (18% vs 28%, respectively; $G = 4.0$, df = 1, $P < 0.05$).

Nest fate varied with habitat ($G = 55.8$, df = 2, $P < 0.001$). Rate of nest disturbance was higher in the forested-patch habitat (49%) compared to either forested-corridor (7%) or contiguous-forested habitats (13%; $G \geq 22.3$, df = 1, $P < 0.001$). The number of disturbed nests in the forested-corridor habitat, however, was similar to that in the contiguous-forest habitat ($P > 0.05$). In contrast, nest fate was not associated with trial or with interactions of two or more variables ($P > 0.05$).

DISCUSSION

We believe that predators did not learn the location of arboreal nests in our study (Eibl-Eibesfeldt 1970, Krebs 1978, Yahner and Wright 1985) because disturbance rates were higher at random than at fixed sites and because rates did not vary among trials. In another study of artificial nests, both avian and mammalian predators preyed upon nests randomly and did not learn the location of experimental nests (Angelstam 1986). In con-

trast, previous work at the Barrens GHMA showed that predators probably learned the location of ground nests at fixed nests in the forested-patch sector, particularly as the study progressed (trials 4 and 5; Yahner and Mahan 1996a).

Because artificial nests pose potential biases and the debate on their usefulness in assessing success of natural nests continues, caution should be used in interpreting the results obtained from artificial nest studies in making management decisions (e.g., Yahner 1996, Ortega et al. 1998, Wilson et al. 1998). Care should be used when extrapolating results obtained from artificial nest studies compared to naturally occurring nests because predation rates on the two types of nests may vary and predation rates may differ among years (Storaas 1988). For example, predators may use behavioral cues from nesting birds to locate naturally occurring nests. Well designed studies using artificial nests remain a useful approach to making inferences about factors affecting avian nesting success, especially when comparisons are made between local habitats, among nests in a given locality, at the same locality over several years, or in detecting trends in rates of predation (Roper 1992, Yahner and Mahan 1996a, Wilson et al. 1998).

Our study and others provided evidence that uncut wooded corridors, which are at least 100 m wide in a forested landscape affected by clearcutting, may provide considerably more secure nesting habitat for breeding birds than small uncut forest stands. For example, Yahner and Ross (1995) found lower predation on Wood Thrush nests in the forested-corridor habitat (50%) than in the contiguous forest (61%) or forested-patch habitats (100%). Based on a study of nest predation along uncut buffer strips retained after clearcutting near streams in Maine, Vander Haegen and DeGraaf (1996) provided evidence that relatively wide (≥150 m) strips enhanced nesting success of forest birds. Their study included artificial ground and arboreal nests containing Japanese Quail (*Coturnix coturnix*) eggs. Despite conflicting evidence for predator learning of the location of artificial arboreal versus ground nests, we recommend that investigators using artificial nests in fragmented forested landscapes carefully randomize nest placement in order to mitigate detection of nests by predators (see Yahner and Mahan 1996a).

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PREDATION ON ARTIFICIAL NESTS ALONG THREE EDGE TYPES IN A NORTH CAROLINA BOTTOMLAND HARDWOOD FOREST

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ABSTRACT.—Many researchers have reported high rates of nest predation near forest edges. However, edges may be of various types (e.g., interior or exterior, abrupt or gradual), which may not always result in elevated predation. We compared predation rates on artificial arboreal nests along three types of edges in a bottomland forest in North Carolina during the 1996 breeding season. Edge types were forest–farm, forest–river, and the transition zone between the two dominant forest types in the floodplain (cypress-gum swamps–natural levees). We tested for differences in predation rates using two egg types: Northern Bobwhite (*Colinus virginianus*) and clay eggs. Predation rates were higher ($P < 0.05$) along forest–farm edges than along the other two edges. Predation rates did not differ between forest–river and transition zone edges. Patterns of predation on the two egg types and higher avian predator abundance on forest-farm edges suggested that avian predators may have exerted more predation pressure along these edges. These results are consistent with other studies, which suggest that encroachment by agriculture into forested landscapes may negatively affect breeding birds. Our findings also suggest that not all edge types are equivalent in terms of predation rates. This is important in assessing the conservation value of bottomland forests, which may contain various edge types resulting from natural processes (e.g., hydrodynamics). *Received 19 Feb. 1999, accepted 6 July 1999.*

Predation is the primary cause of nest loss for a wide range of passerine birds (Martin 1992) and may be the most important factor affecting their population dynamics (Temple and Cary 1988). Forest birds nesting in highly fragmented landscapes or near edges may experience higher rates of nest predation than birds nesting in contiguous forests (Paton 1994, Andrén 1995, Robinson et al. 1995). However, forest edges occur in a variety of contexts which may not always lead to increased predation levels. For example, edges may be in the interior (e.g., clearcuts within contiguous forest) or along the exterior (e.g., agricultural encroachment from outside) of forests and they exhibit varying degrees of contrast from subtle to abrupt (Ratti and Reese 1988, Yahner et al. 1989, Hawrot and Niemi 1996, Fenske-Crawford and Niemi 1997, Suarez et al. 1997). Most researchers reporting high predation rates near edges have examined abrupt exterior edges (reviewed by Andrén 1995). Those that have considered interior and more subtle edges have reported less consistent results (e.g., Ratti and Reese 1988, Yahner et al. 1989, Fenske-Crawford and Niemi 1997, Suarez et al. 1997). Further investigation into the characteristics of edges that influence levels of predation is clearly needed. Such information could be used to assess the conservation value of complex landscapes, such as bottomland hardwood forests that support diverse breeding bird communities (e.g., Wharton et al. 1981, Mitchell and Lancia 1990, Mitchell et al. 1991, Pashley and Barrow 1992). These forested wetlands may contain a variety of edge types that result from the patchwork of plant communities whose arrangement is influenced by site-specific hydrodynamics and sediment deposition rates along floodplains (Wharton et al. 1982).

We compared predation rates on artificial arboreal nests among three edge types in bottomland hardwood forests along the Roanoke River in North Carolina. The three edge types were: (1) forest–farm edge (an abrupt exterior edge), (2) forest–river edge (an abrupt interior edge), and (3) levee–swamp edge (a gradual interior edge where the two dominant plant communities in the floodplain meet). We used artificial nests primarily because of the logistic and experimental advantages afforded by their use. We do not claim that predation rates on artificial nests represent those experienced by natural nests, only that the pattern of predation among edge types are likely to be similar for the two. For example, the few studies that have compared patterns of predation among habitats using both artificial and nat-

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ural nests as well as studies comparing similar habitats using either of these methods have typically found a close match in predation patterns for the two nest types (see Andrén 1995). To our knowledge, this is the first study to examine predation rates at an edge between two relatively undisturbed forested plant communities and only the third to examine a forest edge abutting water (Bollinger and Peak 1995, Vander Hagen and DeGraff 1996). Differences in predator communities among the three edge types were assessed by comparing patterns of predation on two egg types and the abundance of likely avian nest predators.

STUDY AREA AND METHODS

This study was conducted within a contiguous forest corridor along the lower Roanoke River between the towns of Palmyra and Jamesville, North Carolina (36° 9′ N to 35° 50′ N, 77° 20′ W to 76° 53′ W). The forested areas we studied have been undisturbed for more than 60 years. Loss and alteration of forests in the floodplain have come primarily from crop (e.g., peanuts, cotton, wheat) and timber production. The lower Roanoke ecosystem is comprised of 20 vegetative community types (Schafale and Weakley 1990), 2 of which are clearly dominant: cypress-gum swamp and coastal plain levee forests (hereafter swamps and levees, respectively). Swamps are flooded for extended periods throughout the year. The dominant canopy species are water tupelo (*Nyssa aquatica*) and bald cypress (*Taxodium distichum*); Carolina ash (*Fraxinus caroliniana*) is common in the understory (Lynch et al. 1994). Levees occur at slightly higher elevations and are comprised of a diverse mixture of canopy species including American elm (*Ulmus americana*), green ash (*Fraxinus pennsylvanica*), hackberry (*Celtis laevigata*), boxelder (*Acer negundo*), water hickory (*Carya aquatica*), and sweetgum (*Liquidambar styraciflua*). The understory of levees is characterized by pawpaw (*Asimina triloba*), ironwood (*Carpinus caroliniana*), and various vines (Lynch et al. 1994). Although the sizes and shapes of patches of the two forest types are variable, levees generally occur as linear patches close to the river channel formed by the deposition of sediment following flooding events. Farther from the river channel, these forests grade into swamps. Levee–swamp edges are comprised of a mixture of species typical of the two forest types. Forest–river edges are comprised of species typical of levees. Forest–farm edges are dominated by swamp trees, with red maple (*Acer rubrum*) also a dominant species.

Artificial nests were placed along two 1.5 km transects established within each edge type. Survey tape was used to mark 59 25-m intervals (nest site locations 1–60) along each transect. Nests were placed at 50 m intervals beginning at the first survey flag (nest site 1) during trials one and three and beginning at the second survey flag (nest site 2) during trial two. Thus, 30 nests were placed along each transect during each trial. All nests were placed on a suitable substrate within 15 m of the survey flag. Transects along forest–river and forest–farm edges ran parallel to the river and fields, respectively, and were approximately 15 m inside the forest. Levee–swamp edge transects ran along the estimated center of the levee–swamp transition zone. Transition zones were characterized by the presence of bald cypress and water tupelo, wetter soils (often with standing water), and a noticeable opening of the understory. This design resulted in all nests being within 30 m of a habitat boundary. Paton (1994) found that edge effects on nest predation are typically found within 50 m of a habitat boundary; the 30 m distance cutoff we used was well within this range. All transects were separated by at least 2 km and were at least 100 m from any other edge type.

Because predators may respond to artificial nests differently than to natural nests (Major and Kendal 1996), we attempted to mimic as closely as possible the size, color, and locations of nests of Acadian Flycatchers (*Empidonax virescens*), a common breeding species in the floodplain. Several other common breeding species place their nests in similar locations (Lynch et al. 1994). Artificial nests were constructed from commercially available miniature grape vine wreaths (approximately 8 cm outside and 5 cm inside diameters) with bottoms of dried grass or leaves lining wire mesh frames (approximately 4 cm deep). Nests were attached with wire to the fork of a low hanging tree branch, sapling, or shrub at a height of approximately 2.5 m.

Three 15 day trials were run over the course of the 1996 nesting season (30 May–24 July). Fifteen days approximates a typical incubation period for open-nesting passerines in the area. Two egg types were placed in each nest: one Northern Bobwhite egg (*Colinus virginianus*) and one smaller white clay egg ("Plastalina", Van Aken International; approximately 20 × 10 mm) to account for potential biases associated with egg type (Roper 1992; Haskell 1995a, b; Major and Kendal 1996). Eggs were placed in each nest 3–5 days after nests were placed in the field. This was intended to mimic the interval between nest building and egg laying (Marini et al. 1995). We minimized human scent at nest sites by wearing rubber boots and gloves while placing nests and eggs, and while checking nests (Nol and Brooks 1982). Nests were checked for signs of predation on three occasions during each trial (day 5, 10, and 15). We considered a nest to be depredated if either egg was damaged or missing. Predation was attributed to a bird if the clay egg was found with bill imprints and/or the bobwhite egg was found with punctures suggestive of a bill (e.g., as described for crows by Rearden 1951). We considered a nest to be depredated by a large mouthed mammal if bobwhite eggs were found half eaten from one end [suggesting raccoon, *Procyon lotor* (Rearden 1951), or gray squirrel, *Sciurus carolinensis* (C. J. Whelan, pers. comm.)], if chewed up clay eggs were found, or if nests were destroyed (e.g., nest ring gone or pulled apart; Best

and Stauffer 1980). Nests for which tooth imprints or scratches were found on clay eggs, or for which both eggs were found still in the nest or in the immediate vicinity and the clay egg was scratched, were considered to have been depredated by small-mouthed mammals (e.g., *Peromyscus* mice; Major 1991, Haskell 1995b). Although snakes may have also contributed to predation, we were unable to attribute predation events to snakes based on evidence at nest sites.

Birds were censused at 10 count stations located at 150 m intervals along each transect. All birds seen or heard within a 50 m radius and more than 50 m but within the area of interest, over a 10 min interval were recorded (Hutto et al. 1986). One census was conducted along each transect during the morning hours (06:30–09:45 EST) between 20 May and 6 June. Abundance of species likely to depredate nests [American Crow (*Corvus brachyrhynchos*), Fish Crow (*Corvus ossfragus*), Blue Jay (*Cyanocitta cristata*) and Common Grackle (*Quiscalus quiscula*)] was expressed as total detections per point (i.e., all detections, unbounded radius). Although some independence among sampling stations may have been sacrificed by using detections at all distances, each of these were "high-detection-ratio" species (i.e., each had a high proportion of the total detections recorded outside of the 50 m radius count circle), suggesting that detections at all distances within the edge and immediately adjacent habitats were more appropriate for comparisons (Hutto et al. 1986).

Univariate repeated measures ANOVA was used to test for differences in predation rates among edge types (Proc GLM, SAS Institute 1990; Winer et al. 1991). The response variable was the proportion of the 30 nests depredated on each transect. The independent variable was edge type (forest–farm, levee–swamp, and forest–river); trial (1, 2, and 3) and days of exposure (5, 10, and 15) were repeated measures. Prior to analyses the response variable was square root-arcsine transformed to meet homogeneity of variance assumption (Levene's test: $P > 0.05$; JMP, SAS Institute 1994). In order to test for potential biases associated with egg type, we used McNemar's tests conducted separately for each edge type (Proc FREQ, SAS Institute 1990). We tested for differences in selected avian predator abundance among edge types using nested-ANOVA (Proc NESTED, SAS Institute 1990). The response variable was the number of detections of selected avian predators per point. Model terms were edge type and transect [edge type]. Data met homogeneity of variance assumption (Levene's test: $P > 0.05$; JMP, SAS Institute 1994). Differences in abundance of individual species of avian predators among edge types were assessed using Kruskal-Wallis tests (Proc NPAR1WAY, SAS Institute 1990). For species where a significant edge effect was found, *a posteriori* contrasts were computed using the nonparametric all-treatments multiple contrast test described in Hollander and Wolfe (1999). An $\alpha \leq 0.05$ was used for all analyses and values presented are means ± SE. Statistical analyses were performed with JMP (version 3.2.2) and SAS (version 7.0) for Windows.

RESULTS

Predation rates differed significantly among edge types ($F = 11.33$, df = 2, 3; $P = 0.04$) and were higher along the agricultural field–forest edges than along the other two edge types ($F = 22.31$, df = 1, 3; $P = 0.01$; Fig. 1). Predation rates did not differ between forest–river and levee–swamp edges ($F = 0.35$, df = 1, 3; $P > 0.05$). There was no difference in predation rate among trials ($F = 0.05$, df = 2, 6; $P > 0.05$). Within trials, predation rate increased with day of exposure ($F = 94.54$, df = 2, 6; $P < 0.001$). Interaction between day of exposure and edge type was nearly significant ($F = 3.55$, df = 4, 6; $P = 0.08$). This nearly significant interaction was likely caused by differences in response pattern (slope) between levee–swamp and forest–river edges from 5–10 days of exposure (Fig. 1). The difference among these two edges at 5 days of exposure was not significant ($F = 5.23$, df = 1,3; $P > 0.05$). Predation rates were highest along forest–farm edges regardless of exposure time.

The number of nests for which the bobwhite egg was damaged or missing was highest on forest–farm edges, while the number of nests for which only the clay egg was depredated was similar among edge types (Fig. 2A). Bobwhite eggs were preyed upon more frequently on forest–farm edges than on the other two edge types (Fig. 2B). Conversely, the percentage of depredated nests in which only the clay egg was preyed upon was lowest on forest–farm edges and highest on levee-swamp edges. For each edge type, the clay egg was depredated significantly more often than the bobwhite egg in nests where only one egg was depredated (Forest–farm: $G_{adj} = 9.49$, df = 1; $P < 0.01$; Forest–river: $G_{adj} = 19.15$, df = 1; $P < 0.001$; Levee–swamp: $G_{adj} = 45.83$, df = 1; $P < 0.001$). Despite this egg type bias, the pattern of predation, higher on forest–farm edges than on the other two edge types, was the same regardless of whether predation was on bobwhite or clay eggs (Fig. 2A).

We identified nest predators for 30% of depredated nests (114/368). Of these, 69% (79) were birds, 22% (25) were smaller mouthed mammals, and 9% (10) were larger

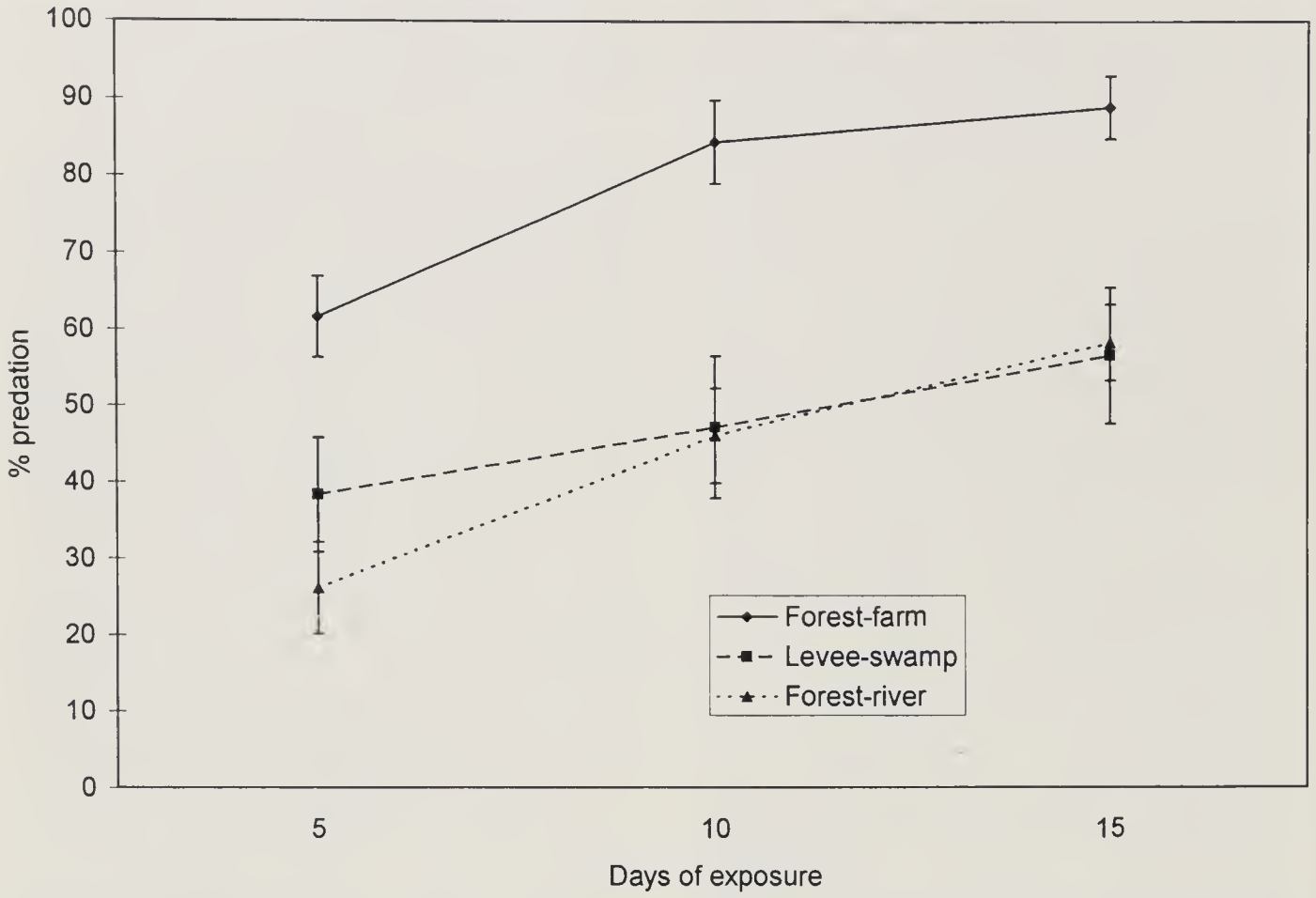

FIG. 1. Predation rates on artificial nests at three edge types in bottomland hardwood forest along the Roanoke River floodplain, North Carolina during the 1996 breeding season. Predation rates were significantly higher along the forest-farm edges than on the other two edges ($P < 0.05$).

mouthed mammals. Although measurements of bill imprints in clay eggs were not taken, the size and shape of these imprints suggested that crows, Blue Jays, and Common Grackles were among the avian predators. The abundance of these nest predators differed by edge type ($F = 36.84$, df = 2, 3; $P < 0.01$) and was higher on forest–farm edges than along forest–river and levee–swamp edges ($F = 65.79$, df = 1, 3; $P < 0.01$; Fig. 3). Avian predator abundance did not differ significantly between forest–river and levee–swamp edges but tended to be higher along the forest–river edge ($F = 7.89$, df = 1, 3; $P = 0.07$; Fig. 3). Considered individually, the four predator species were not consistent in their responses to edge type (Fig. 3). The numbers of American and Fish Crows detected differed significantly among edge types (American Crow: $\chi^2 = 11.21$, df = 2, $P < 0.01$; Fish Crow: $\chi^2 = 12.27$, df = 2; $P < 0.01$), and both of these species were significantly more abundant along forest–farm edges than along levee–swamp edges (American Crow $q = 4.28$, Fish Crow $q = 4.42$; $P < 0.01$). American Crows were also significantly more abundant on forest–farm edges than along forest–river edges ($q = 3.65$; $P < 0.05$). Fish Crows tended to be more abundant along forest–farm edges than along forest-river edges, although this difference was not significant ($q = 3.06$; $0.05 < P < 0.10$). In contrast, Blue Jays, which also showed a significant edge effect ($\chi^2 = 6.05$, df = 2; $P < 0.05$), were more abundant along forest-river edges than on levee-swamp edges ($q = 3.33$; $P < 0.05$). Contrasts between forest-farm edges and the other two edge types for this species were not significant ($P > 0.05$). Common Grackle abundance did not differ significantly among edge types ($\chi^2 = 3.74$, df = 2; $P > 0.05$).

DISCUSSION

Our findings are consistent with most previous studies that have reported high rates of nest predation along abrupt exterior edges (our forest–farm edge type; see Andrén 1995). The presence of more avian predators along

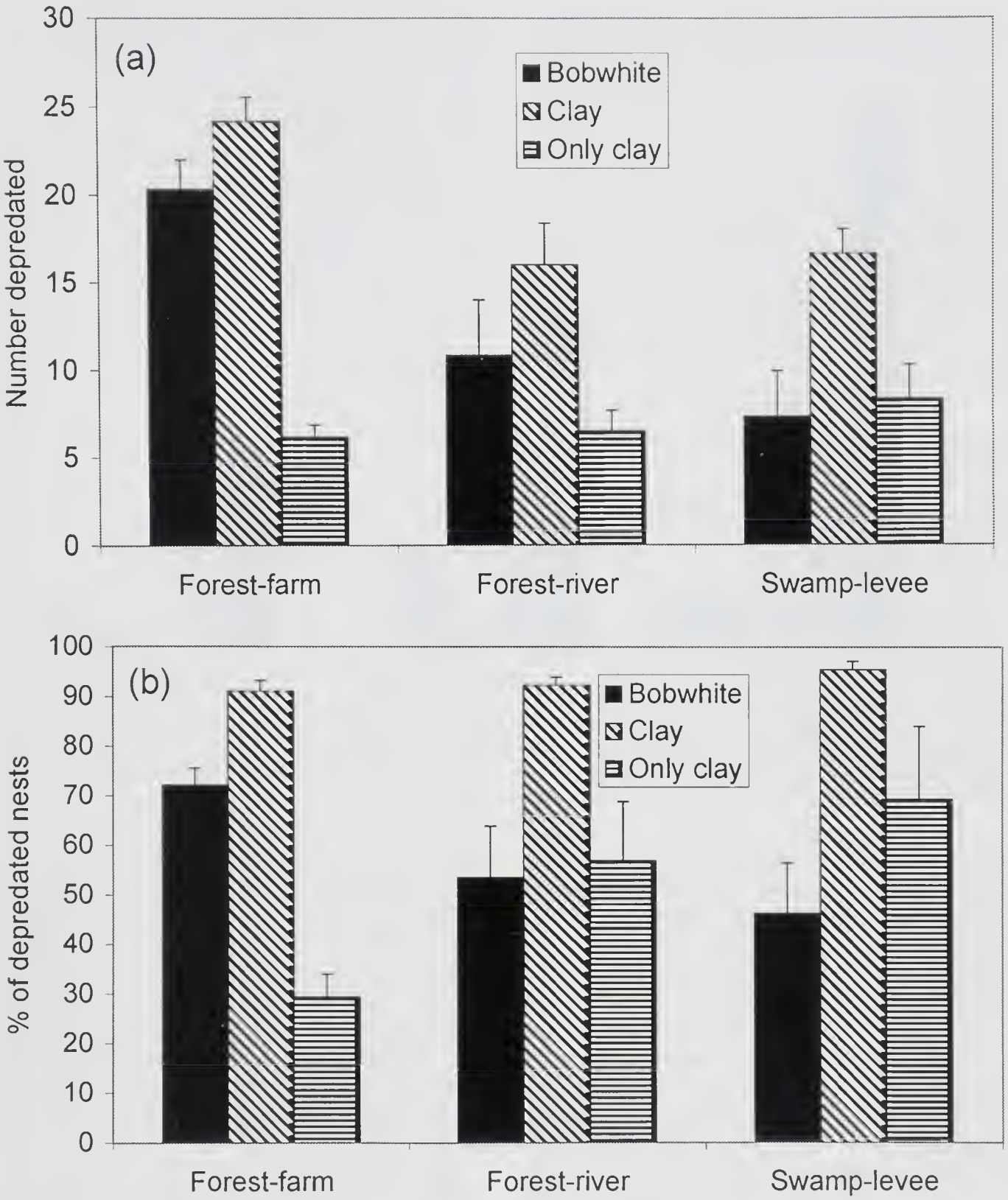

FIG. 2. (A) Absolute number of depredated nests and (B) the percentage of depredated nests for which the bobwhite egg, clay egg, or only the clay egg was preyed upon. Results of McNemar's tests conducted for each edge type (n = 180 nests) suggested a significant egg type bias ($P < 0.01$ for each edge type); however, the same pattern of predation (highest on forest-farm edges) was apparent regardless of whether bobwhite or clay eggs were considered.

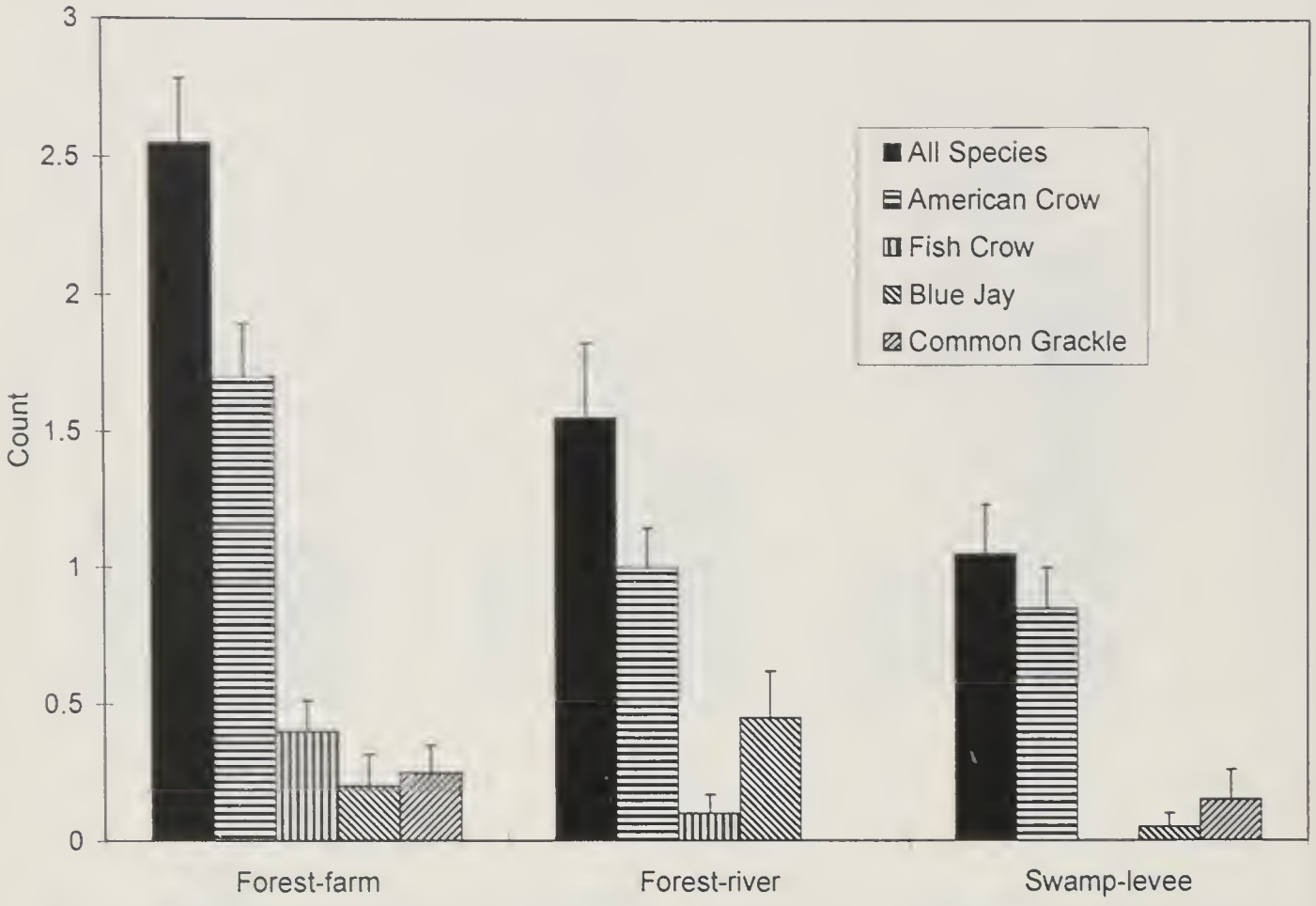

FIG. 3. Mean number of detections per point for selected avian nest predators at three edge types in a bottomland hardwood forest along the Roanoke River floodplain, North Carolina. The pooled abundance for all species was significantly higher on forest–farm edges than on the other two edge types ($P < 0.01$); the responses of individual species were not consistent among edge types.

forest–farm edges may have contributed to the higher predation rates we observed along these edges. Marini and coworkers (1995) found a positive correlation between avian predator abundance (American Crows, Blue Jays, and Common Grackles) and predation levels on artificial nests in forest saplings, as well as significantly higher predation rates on these nests at forest–farm edges. Other researchers have also related avian nest predator abundance (e.g., corvids) to forest–farm edges or shown predation on artificial nests by these predators to be higher near such edges (e.g., Whitcomb et al. 1981, Angelstam 1986, Andren 1992, Nour et al. 1993).

Our finding that nests at forest–river edges experienced lower predation rates than forest–farm edges is in accordance with Vander Haegen and DeGraff (1986) who found no effect of distance from a river edge on predation rate. In contrast, Bollinger and Peak (1995) found predation rates to be uniformly high on artificial ground nests along a forest edge bordering water and a forest–farm edge in one forest fragment in an agricultural setting. Small forest fragments in agricultural landscapes such as this may become inundated with certain mammalian predator species (e.g., raccoons; gray squirrels, *Sciurus carolinensis*; and opossums, *Didelphis marsupialis*; Bider 1968, Matthiae and Stearns 1981). The relatively wide and heavily forested river corridor in our study may have alleviated any such packing effects by predators.

The levee–swamp edges we studied are unique in that they are naturally occurring boundaries between plant communities rather than edges resulting from human activities (e.g., agriculture, forestry practices). As such, they may not be perceived as edges by some predators that may move freely between levees and swamps rather than concentrating activities along the edge or using it as a travel lane (Bider 1968, Chasko and Gates 1982). This could explain the relatively low predation rates we observed at these edges.

It is difficult to determine the relative impact of different predators at the three edge types because predators were only identified for 30% of depredated nests. The greater abundance of avian predators at forest–farm edges may have contributed to the higher predation rates there; however, some mammalian predators and snakes might also be abundant and concentrate their activities or travel along abrupt edges (Bider 1968, Chasko and Gates 1982, Durner and Gates 1993; but see Heske 1995). Unfortunately, we were unable to assess the relative abundance of non-avian predators or their relative contribution to predation on artificial nests. Nonetheless, there was some indication that the predators responsible for depredating nests may have differed among edge types. For example, because small mouthed predators may have been unable to damage the Northern Bobwhite eggs [as has been reported for Japanese Quail (*Coturnix coturnix*) eggs; Roper 1992, Haskell 1995a], our finding that the proportion of nests for which only the clay egg was depredated was higher at the forest interior edges suggests that small mouthed predators (e.g., mice) may have been more important at these edges. In contrast, both the proportion and absolute number of depredated nests for which the bobwhite egg was preyed upon was highest at forest-farm edges. This supports the contention advanced by Haskell (1995b) and Nour and coworkers (1993) that avian and larger mammalian predators increase in importance in small forest patches or at the edges of forests. Smaller mouthed predators, although possibly more frequent at the interior edges, appear to have depredated similar proportions of nests along the three edge types. Finally, differential predation rates at different types of edges could also be influenced by factors other than the types of predators involved and their abundance. Future studies should be designed to consider factors influencing nest site selection (e.g., number of potential nest sites) and nest densities of avian community members (Martin 1993).

Bottomland hardwood forests of the southeastern U.S. are being destroyed and fragmented at high rates (Turner et al. 1981, Abernathy and Turner 1987). These areas provide important breeding habitats for many migratory and resident birds (Wharton et al. 1981, Mitchell and Lancia 1990, Mitchell et al. 1991, Pashley and Barrow 1992). Understanding how edges resulting from natural processes (e.g., hydrodynamics), as well as from anthropogenic modifications, affect breeding bird communities is important to their conservation and management. Our results suggest that encroachment by agriculture may negatively affect breeding birds through higher predation rates along forest–farm edges. Natural edges between adjacent plant communities and at the forest–river interface may not affect breeding birds in the same way.

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THE RESPONSE OF A KANSAS WINTER BIRD COMMUNITY TO WEATHER, PHOTOPERIOD, AND YEAR

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ABSTRACT.—We conducted a bird census along the same route nearly each week for 14 winters (194 censuses), and compared the mean number of species per station and the total number of species recorded on the census with the length of photoperiod and weather variables. We found significant differences among winters for both indicators of species richness. This result is consistent with previous studies in which abundance of food was measured in the same general area. Both indicators of species richness were negatively associated with the number of days after 1 November. This result is consistent with the hypothesis that wintering species dependent on nonrenewed food resources lose individuals to mortality or emigration. Further, there was a positive relationship between photoperiod and both indicators of species richness. This result is consistent with the hypothesis that the detection of individuals in the early morning hours increases with the amount of daylight they have available for foraging and social behaviors. Wind speed and temperature had negative and positive relationships, respectively, to species richness. The number of species per station was greatest on days when the ground was covered with dew and least on days when snow depth was more than 15 cm. When the "winters" were divided into four 30-day "quarters", most of the 61 species were recorded with equal frequency in each quarter. Eight species were detected less frequently at the end of winter than in the beginning. Four species exhibited the reverse pattern. Two species were recorded more frequently at the beginning and at the end of the winter than during the middle. Temperature, wind, photoperiod, successive winter day, year, and species-specific evolutionary history all affect winter bird species richness. *Received 1 Oct. 1998, accepted 5 August 1999.*

Winter is a stressful season of the year for endotherms at mid- and high latitudes. Severe cold, short photoperiod, and a mostly nonrenewed food supply make it a challenge to maintain a constant body temperature. Many bird species migrate to more hospitable climates. For those species that overwinter at higher latitudes, weather conditions have been shown to affect the amount of body fat stored (White and West 1977, Dawson and Marsh 1986, Peach et al. 1992, Waite 1992, Houston and McNamara 1993, Rogers et al. 1994, Pilastro et al. 1995). Collins (1989) provided a short review on some of the major physiological adaptations in birds for surviving the winter. Robbins (1972, 1981a) and Altman (1983) discussed the importance of weather conditions on winter bird populations.

Although detailed, long-term winter studies exist for specific species (Loery and Nichols 1985), data for studies of overwintering bird communities often are collected only for a few days per year (cf., Erskine 1992). For example, three counts per year are made for the Finnish winter bird census routes (Hildén 1987), and the Christmas Bird Count is an annual one-day count of an area. The daily effects of weather components and the annual effects of available food resources (e.g., mast crop failure) on the number of species in an area are often difficult to determine or are statistically confounded. Instructions for the Winter Bird-Population Study (Robbins 1981b) call for a minimum of six visits per site per year. However, daily weather data for the study sites and analyses of the effects of weather components on species richness are typically lacking (Robbins 1981a). Further, depending on species-specific responses to abiotic factors and food abundance, bird species may differ in their detectability during the course of winter.

We analyzed data from bird censuses conducted at nearly weekly intervals for 14 years (194 censuses) along the same route. We include in our analyses weather data collected from a permanent station approximately 10 km from the route. Our objectives were to (1) quantify the effects of weather components, photoperiod, and the cumulative number of

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winter days on species richness; and (2) to determine if the frequency of detection of individual species changed over the course of the winter. To accomplish the first objective, we used a statistical procedure that accounts for the correlation structure (i.e., time-dependency) between censuses taken within each winter. We accomplished the second objective by testing the null hypothesis that individual species were recorded with equal frequency within each of four 30-day intervals during the winter.

METHODS

Census route and field method.—Our study, like others based on seeing and/or hearing birds to count their presence, measured the visual and auditory detectability of birds. Birds were counted with a modified Breeding Bird Survey procedure (Robbins et al. 1986) along a regular census route across the border between Riley and Pottawatomie counties, Kansas (Stapanian 1982, Stapanian et al. 1994). The route consisted of 16 stations; unlike the Breeding Bird Survey routes, the stations were not separated by regular 0.81 km intervals. Instead, stations were selected to represent typical upland and riparian forest habitats with some tree species bearing fleshy, bird-dispersed fruit in proportion to their presence in the Kansas Flint Hills. Nine stations were along one road and seven were along another. There were eight convenient sequences in which the 16 stations could be visited. Each of the eight sequences of stations was used during eight consecutive censuses. Therefore, there was no consistent pattern in the time after official sunrise that each station was visited. Distances between stations on the same road ranged from 0.3 to 1.6 km (mean = 1.0). The nearest stations on the two roads were separated by 13 km. Because our goal was to quantify the effects of weather, photoperiod, and cumulative number of winter days on species richness in the entire area, data were pooled for all stations. Birds were identified to species, and the number of individuals was counted for 3 min at each station. Birds flying overhead were included in the analysis. Censuses were conducted at approximately weekly intervals November–February, 1982–1996. Each census began within 1 h after sunrise and required approximately 2 h to complete. In accordance with instructions for Breeding Bird Surveys (Robbins 1981b), no censuses were conducted in fog, steady drizzle, prolonged rain, or winds stronger than Beaufort 3 (13–19 km/h).

In selecting stations for the census, the original criterion was a wooded area with concentrations of trees of *Juniperus virginiana, Morus rubra,* or *Celtis occidentalis* that would attract frugivorous birds (Stapanian 1982). The two roads along which the stations were spaced held a variety of habitats (Table 1), which affected our bird censuses. At each station we visualized a line perpendicular to the road and classified each of the four 90° sections thus formed as being predominantly in one category for Table 1. Thus, there are a total of 64 sections for the 16 stations that form Table 1. The Flint Hills area of Kansas held almost no forests before European settlement (Axelrod 1985). Only about 16 species of native trees have spread into the area from the eastern deciduous forests after the control of prairie fires. Two stations were completely surrounded by forest, but 14 stations had at least one 90° section of forest holding one of the three tree species producing fleshy fruit and the other two stations had fence rows with *M. rubra.* The mature forests are separated into those with and without bur oaks (*Quercus macrocarpa*) because this tree species must have a large acorn crop in order for Red-headed Woodpeckers (*Melanerpes erythrocephalus*) to winter in the area. Some of the residences near stations on the census were homes with lawns while others had corrals for livestock. At five stations birds could be heard calling from mature forests beyond extensive fields of row crops (Table 1).

TABLE 1. Habitat type for census stops by the number of stops at which the habitat was represented and by the number of 90° arcs at the 16 stops that were predominantly composed of that habitat.

Habitat	Number of census stops	Number of 90° arcs
Native prairie	1	1
C_3 grass pastures	5	6
Row crops	7	13
Residential and farm buildings	7	9
Dense shrub	2	4
Juniper forest	4	4
Young mixed forest	7	12
Mature mixed forest with oak	3	6
Mature mixed forest without oak	2	6
Riparian margin forest	2	3
Forest beyond crops	5	—

Although our survey has been conducted along the same route nearly every week since 1978 (Stapanian et al. 1994), because weather data are not available before 1982, we only analyzed data from November 1982 through February 1996. We selected the period between 1 November through 28 February because it represents a time interval in the study area during which (1) food sources are not renewed and (2) Neotropical migrants are rarely present. We divided this interval into four 30-day periods (quarters) for analysis of the presence of individual species. Our censuses were designed to monitor populations of upland birds (Stapanian 1982, Stapanian et al. 1994). Aquatic and nocturnal species were eliminated from the present analysis. For each census, we calculated the mean number of species recorded per station and the total number of species recorded from all stations.

Our procedures differed from Breeding Bird Surveys in three ways. First, when no birds were evident

at a station, we spished to attract them. Second, when we were unable to find new birds where the car was parked, we walked along the road in search of birds. Third, we had more than one observer on 58% of the censuses. Neither of the first two differences biased the data. Making noise and walking along the road when no birds were evident would tend to overestimate the number of bird species and individuals when they were lowest. Thus, any conclusions we would make about which factors decreased bird activity and the number of species would be conservative. The number of observers ranged from one (82 censuses, 42.1%) to four (3 censuses, 1.5%). The number of censuses in which there were two and three observers were 81 (41.5%) and 29 (14.9%), respectively. In exploratory analyses, we found that the number of species recorded was greater when more than one observer participated in the census. Therefore, we adjusted mean species per station and total species per census for the number of observers. In controlled experiments performed during winter on this route (C. C. Smith, unpubl. data), we found that the mean number of species per station and total species per census increased on average by factors of 1.32 and 1.08, respectively, for multiple observers over those values found by one observer. Thus, when the number of observers was greater than 1, we divided mean species per station and total species per census by 1.32 and 1.08, respectively. Further, C.C.S. participated in all censuses and his hearing still allows him to detect a Brown Creeper (*Certhia americana*) at 30 m. E.J.F. participated in almost all censuses from 1982 through February 1989. J. Cavitt, S. Hansen, S. Hull, C. Pacey, G. Radke, and C. Rebar participated in at least four censuses each.

Weather data.—Weather data for each census were collected automatically from a permanent station at the Konza Prairie Research Natural Area, located within 18 km from all our census stations. The weather station measured wind speed at hourly intervals on the hour. We, therefore, selected weather data recorded at 07:00 on each census day. Because each census began within 1 h after official sunrise, 07:00 does not represent a standard time relative to sunrise for all censuses. However, we were confident that the data were representative of the weather during our censuses.

We use a standard weather service formula to convert temperature and wind speed to a wind chill temperature. Wind chill temperature exceeded air temperature only for wind speeds greater than 6.7 km/h, which occurred on only six censuses. In exploratory analyses of variance, we found that of the weather variables recorded, only temperature and wind speed accounted for a significant proportion of the variance in our statistical models.

We ranked ground conditions from 1 though 6 according to what we perceived as increased difficulty for birds in finding food on the ground: (1) dry, (2) dew, (3) frost, (4) wet from rain or melting snow, (5) snow 15 cm or less deep, and (6) snow more than 15 cm deep. Ground condition was recorded at the first station we visited on all but six censuses. All stations were then assigned the same weather data and ground condition class as the first station for the census.

Statistical analyses.—"Winter day" was designated as the number of days after 31 October for each census. Photoperiod was calculated from published tables (U.S. Naval Observatory 1945) as the number of minutes between official sunrise and official sunset on each census date, and ranged from 565 to 679 min.

We tested for the effects of winter day, photoperiod, and weather components on our two indicators of species richness. In exploratory analyses and previous studies (Stapanian et al. 1994) we found considerable variance in the species richness among winters. Further, we found significant time dependency among the successive censuses within winters. Therefore, we used a mixed models procedure (Crowder and Hand 1990, SAS Institute 1992, Littell et al. 1996) in which each winter was treated as a random effect (i.e., whole plot), and the remaining variables were treated as fixed covariates (i.e., subplots) to account for the correlation structure among the censuses within winters. The degrees of freedom and mean squares were adjusted for time dependency based on the covariance structure and inference space. Ecologically, this meant that we removed winters as a random effect from the statistical model tests for the effects of the fixed covariates based on an average set of conditions at the beginning of winter. The resulting model was general, not winter-specific.

We evaluated the covariance structure in three ways: (1) uniform correlation (compound symmetry), (2) exponentially decaying, and (3) Markov chain. In exploratory analyses, we found that the uniform correlation method best represented the covariance structure of the data set. Further, we found that none of the two-way interactions between the fixed covariates contributed significantly to the models ($P > 0.05$ in all cases). Thus, we performed the mixed models analyses only on the main effects of the fixed covariates. We performed Tukey's tests for *a posteriori* testing on the effects of specific ground condition classes on diversity.

We defined ordinal year as the ordinal number of a census year (i.e., year 1 = 1982–1983, year 2 = 1983–1984, . . . , year 14 = 1995–1996). We performed standard Pearson correlations between ordinal year, species richness, and our weather variables. In this manner, we were able to test for overall temporal trends in weather and diversity on census days on our census route.

For each species, we calculated the proportion of the censuses conducted in each quarter (30-day interval) of each year in which that species was recorded (Appendix). These quarterly proportions were then pooled across all 14 winters for each species. Using analysis of variance, we then tested the null hypothesis that each species was recorded in equal proportions in all four quarters. Tukey's pair-wise comparisons were used for all *a posteriori* testing. SAS for Personal Computers, version 6.12 for Windows was used for statistical computations.

TABLE 2. Summary statistics for each winter for the total number of species recorded on each census and the mean number of species per station on each census. These variables were adjusted for number of observers. Years that share a grouping letter were not significantly different (Tukey's pair-wise comparisons, $P > 0.05$) for that indicator of diversity.

		Species per census		Species per station	
Year	n[a]	Mean	SD[b]	Mean	SD[b]
1982–1983	12	24.18	2.29 B, C, D	5.00	0.74 A, B, C
1983–1984	14	18.21	4.97 E	3.52	1.54 D, E
1984–1985	14	19.48	2.65 D, E	3.99	1.02 C, D
1985–1986	13	23.40	3.32 B, C	5.04	1.44 A, B, C
1986–1987	11	22.09	3.67 B, C, D, E	4.89	1.02 A, B, C, D
1987–1988	12	23.73	2.59 B, C	5.50	1.18 A, B
1988–1989	14	24.45	2.07 B, C	5.37	0.91 A, B
1989–1990	15	23.75	4.16 B, C	4.98	0.59 A, B, C
1990–1991	14	25.93	2.76 B	5.86	1.09 A
1991–1992	15	18.39	3.26 E	3.65	1.25 D
1992–1993	15	23.71	2.99 B, C	4.97	1.07 A, B, C
1993–1994	16	29.81	3.67 A	5.36	1.12 A, B
1994–1995	13	24.00	2.16 B, C	5.34	1.36 A, B
1995–1996	16	22.32	1.37 C, D	4.63	0.95 B, C, D

[a] n = number of censuses.
[b] SD = standard deviation.

RESULTS

There were significant differences among winters for the annual means of both total species per census and species per station ($F_{13,180}$ = 13.87 and 5.46, respectively, $P < 0.001$ in both cases; Table 2). Consequently, we treated winters as random effects in our mixed model analysis. The results from the mixed model procedure (Table 3) suggested significant effects from winter day, photoperiod, temperature, and wind speed for the number of species per census and species per station. Temperature and photoperiod were positively related to both indicators of species richness when the covariance structure was taken into account (slopes in Table 3). On the other hand, wind speed and winter day had negative effects on both indicators of diversity (slopes in Table 3). On average, a change of 1° C in temperature or 1 km/h in wind speed had a greater effect on species richness than did either a change of 1 min in photoperiod or 1 day further into winter.

Ground condition had a significant effect on species per station, but not on species per census in the mixed model analyses (Table 3). Values of species per station were lowest when there was more than 15 cm of snow on the ground and greatest when the ground was covered with dew (Table 4).

Both of our indicators of species richness increased over the course of our study. There was weak but positive correlation between species per census and ordinal year (r = 0.27, df = 12, $P < 0.001$) and between species per station and ordinal year (r = 0.15, df = 12,

TABLE 3. Results of the mixed models ANOVA procedure. Two-way interactions were not found to be significant in exploratory analyses ($P > 0.05$). Slopes and standard errors (SE) of the slopes are not reported for ground condition because it was not a continuous variable.

		Species per census				Species per station			
Source	df	F	$P > F$	Slope	SE	F	$P > F$	Slope	SE
Winter day (days)	1	20.35	0.001	−0.033	0.007	21.89	0.0001	−0.011	0.002
Photoperiod (minutes)	1	11.51	0.0009	0.029	0.008	40.03	0.0001	0.017	0.003
Temperature (° C)	1	7.65	0.0063	0.111	0.040	30.53	0.0001	0.070	0.013
Wind speed (km/h)	1	26.36	0.0001	−0.634	0.123	45.86	0.0001	−0.264	0.039
Ground condition	5	1.10	0.3636			2.54	0.0301		

TABLE 4. *A posteriori* tests (Tukey's pair-wise comparisons) on the effects of ground condition on the mean values of the mean number of species per station on a census. Means of ground condition classes with at least one letter in common are not significantly different ($P > 0.05$).

Ground condition	Class	n[a]	Mean of mean species per station
Clear, dry	1	53	4.93 B
Dew	2	10	6.12 A
Frost	3	39	5.14 B
Wet	4	31	4.75 B
Snow ≤ 15 cm	5	50	4.47 B
Snow > 15 cm	6	5	3.56 C

[a] n = number of censuses.

$P = 0.035$). Further, there was a weak but negative correlation between wind speed and ordinal year ($r = -0.16$, df = 12, $P = 0.022$), which suggested that wind speed on census trips decreased over the course of this study. We made no conscious change in our policy of when to hold censuses during our study that would have resulted in lower wind speeds during censuses. Neither temperature nor ground condition class was significantly correlated with ordinal year ($P > 0.05$ in both cases).

Sixty-one species were recorded for our study (Appendix). Only two species, American Crow (*Corvus brachyrhynchos*) and Black-capped Chickadee (*Poecile atricapillus*), were recorded on all 194 censuses. Twenty-two species (36.1% of the total species) were recorded on at least 50% of the censuses. Thirteen species (21.3% of the total species) were seen on less than 5% of the censuses. There was no consistent pattern to the temporal occurrences of individual species (Appendix). For most species, the proportion of the censuses in which they were recorded was the same for each quarter. Eight species, Northern Flicker (*Colaptes auratus*), Golden-crowned Kinglet (*Regulus satrapa*), Northern Bobwhite (*Colinus virginianus*), White-crowned Sparrow (*Zonotrichia leucophrys*), Common Grackle (*Quiscalus quiscula*), Field Sparrow (*Spizella pusilla*), White-throated Sparrow (*Zonotrichia albicollis*), and Lincoln's Sparrow (*Melospiza lincolnii*), occurred more frequently in early winter than in late winter. The reverse trend was exhibited by four species, American Tree Sparrow (*Spizella arborea*), Tufted Titmouse (*Baeolophus bicolor*), Western Meadowlark (*Sturnella neglecta*), and Eastern Meadowlark (*Sturnella magna*). Two species, Red-winged Blackbird (*Agelaius phoeniceus*), and Ring-necked Pheasant (*Phasianus colchicus*), were recorded less frequently in mid-winter (i.e., in the second and third quarters) than at the beginning or end. Species observed on fewer than 5% of the censuses were not considered common enough to test for patterns of occurrence by winter quarter (Appendix).

DISCUSSION

Our study is the first of which we are aware that demonstrated significant effects of photoperiod, cumulative number of winter days, and weather components on bird species richness of upland and riparian forest birds in winter. The results appear to differ considerably from those of Robbins (1981a). He detected no effects of weather conditions on the numbers of selected species or families of birds from repeated coverage of a Winter Bird Survey route. Robbins' 8-km route in Maryland was covered at least three times per year for five consecutive years in late December or early January. He also analyzed data from eight years of Audubon Winter Bird-Population Studies on two forest plots in Maryland. There were no significant effects of temperature on the number of species he recorded. The differences between our results and those from Robbins may be due to (1) our larger sample size, (2) a longer season (i.e., November through February) in our study, (3) the fact that Robbins' (1981a) analyses were restricted to selected species and families, or (4) differences in location and climate. Most importantly, Robbins (1981a) selected for calm, dry mornings in both studies. Therefore, it is not surprising that he reported no weather effects on the number of species recorded.

Although ours is a long-term study, there were too few censuses to analyze the effects of number of winter days, photoperiod, and weather on species richness for specific winters. The data strongly suggest that differences in the detection of bird species occurred among winters. Previously, we (Stapanian et al. 1994) estimated extremely low seed crops for weeds, herbs, grasses, and bur oak for the winters of 1983–1984 and 1984–1985. Simi-

larly, we estimated extremely low weed seed and wild fleshy fruit crops for the winter of 1991–1992. These low food supplies may partly explain why the fewest species were recorded in those years. Large crops of herb and grass seeds were estimated for the winter of 1982–1983, which had relatively high values for species per station. Similarly, there were large crops of acorns and fleshy fruits for 1988–1989 and 1990–1991. In both winters, species richness was relatively high. These trends support the importance of the size of unrenewed food supplies in determining the detection of winter bird populations.

By treating the large winter differences as random effects, the statistical analysis demonstrated that photoperiod affects the morning activity of birds. The influences of photoperiodism on the physiology and activity of birds are well documented (Bissonette 1932, 1937; Bartholomew 1949; Welty and Baptista 1988 and references therein; Ball 1993; Hau et al. 1998). Perhaps when less time is available for feeding, as in mid-winter, birds spend less time in easily detected behaviors. The behavioral effect of reduced feeding time relative to energy needs is likely to be larger flock size (Caraco 1979, Sullivan 1988) and a lower probability of seeing birds at the average station.

Temperature and ground condition classes were significantly and negatively correlated ($r = -0.37$, $P < 0.001$, $n = 187$). Thus, what we perceived as difficult foraging conditions might have been simply a consequence of low temperature. Dew (ground condition class 2) and ground wet from rain or snowmelt (class 4) required that the air temperature exceed 0° C, while the temperature may be below 0° C for dry ground (class 1) and will be for frost (class 3). When we switched the number class of frost to 4 and rain or snowmelt to 3, the correlation coefficient between temperature and ground condition class increased in absolute magnitude ($r = -0.508$, $P < 0.001$). Ground condition may have little effect independent of temperature.

We are not sure how to interpret the negative effects of wind speed on bird species per census or bird species per station. Wind speed had a negative effect on both indicators of species richness even when we considered only those censuses in which wind speeds were less than 6.7 km/h, the speed above which wind chill temperature is less than air temperature. The effects of wind speed on species richness appear to be due to neither a decrease in our ability to hear birds, nor apparent additional thermoregulatory stress for the birds. However, wind speed typically increases after sunrise, and the wind speed at the end of a census may be greater than at the beginning. Small differences in wind speed at 07:00 may be magnified later in the census. There is evidence that some species, particularly those with small body sizes, can reduce metabolic demands in winter by selecting microhabitats that are sheltered from the wind and exposed to solar radiation (Wolf and Walsberg 1996).

Similarly, we are unsure why both indicators of species richness increased in later years. The same principal observer (C.C.S.) was present for all censuses in our study. Eyesight and hearing typically deteriorate over time (Cyr 1981), but these effects can be countered by individual experience with a specific route. The increases in species richness were not due to changes in mean annual temperature, because temperature and ordinal census year were not significantly correlated ($r = 0.109$, df = 12, $P > 0.05$). Wind speed on the census trips was negatively correlated with year and with both indicators of species richness. Thus, a decrease in wind speed on census days may partially explain the increases in species per station and species per census over the census years. Species composition on the census route changed over time. For example, the population of Carolina Wren (*Thryothorus ludovicianus*), a sedentary bird species, increased steadily during the 14 years of the census after a time when it was at low levels in the Manhattan Christmas bird counts. Wild Turkeys (*Meleagris gallopavo*) were reintroduced in the area in the early 1980s and their populations have increased since. These changes may be due to milder winters during the study period. There may have been an increase in canopy closure or structural diversity of the habitat on the route over the 14 years of the study, but that was not measured.

White-crowned Sparrows and White-throated Sparrows feed in large mixed flocks of sparrows in late winter and in smaller groups in late fall. These species were recorded on a

greater proportion of the censuses in the first quarter than in any other. November (first quarter) typically has the mildest average weather of any quarter and food abundance should be greatest at this time. Therefore, the selective pressure on birds for being in large flocks should be least at this time (Caraco 1979, Sullivan 1988). If members of a species were more widely distributed geographically, an observer would be more likely to record that bird species at least once on a census. Field Sparrows, Lincoln's Sparrows, and Common Grackles were also seen with greater frequency in November than in late winter. The Kansas Flint Hills are along the northernmost edge of the winter range of these three species (Thompson and Ely 1992). Although most members of these species migrate south out of the census area, a few overwinter (Zimmerman 1993). The decrease in numbers for these species during the winter could be a result of continued migration south or mortality in a marginal range.

The proportions of censuses on which Northern Bobwhite (a resident species), Golden-crowned Kinglet (a winter migrant), and Northern Flicker (winter resident and winter migrant; Thompson and Ely 1989, 1992; Zimmerman 1993) were recorded dropped steadily from the second through the fourth quarter. This decline may have been due to mortality to the wintering populations of those species. The results from our study for Golden-crowned Kinglet agreed with those of Zimmerman (1993) who hypothesized that the variation in departure of Golden-crowned Kinglets from the area was related to availability of food.

Eastern Meadowlark, Western Meadowlark, and Tufted Titmouse were recorded most frequently on censuses in the last quarter. These are resident species (Thompson and Ely 1992, Zimmerman 1993) that breed early in spring and begin establishing territories and/or obtaining mates in late winter. The American Tree Sparrow, a winter migrant to the area (Zimmerman 1993), was recorded least frequently in the first quarter. This agrees with Finck (1986), who found this species to be most numerous from December through February, suggesting a late migratory arrival. Red-winged Blackbird and Ring-necked Pheasant were most often recorded in November and February. These are resident or partly resident species that flock in severe weather in mid-winter. However, they begin preparation for breeding in late winter (Zimmerman 1993). Zimmerman (1993) found Red-winged Blackbird to be "occasional" during the winter months of most years in upland habitats until the migrants returned in late winter.

Our results are consistent with at least five hypotheses: (1) species are lost by mortality resulting from nonrenewed resources over the course of winter, (2) resident species move in and out of detection distance in the census area, (3) selective pressures for flock sizes change with weather conditions and food abundance, (4) some species are more easily detected in late winter because of early courtship behavior, and (5) species richness in the census area changes as a result of the arrival and departure of seasonally migrant species. The results suggest a complex relationship among weather components, photoperiod, abundance of resources, and species-specific evolutionary histories on winter bird species richness. We suggest further studies to analyze responses by individual species to resource abundance and abiotic factors in winter.

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APPENDIX

The number of all censuses (All) and the mean proportion of censuses in 30-day intervals over 14 winters in which species were observed. For each species, we tested the null hypothesis that it was recorded in equal proportions in all four quarters. *A posteriori* tests (Tukey's pair-wise comparisons) were performed on those species for which the null hypothesis was rejected. Quarterly means for a species having the same letter were not significantly ($P < 0.05$) different. Species listed at the bottom lacked significant quarterly differences. Abbreviations: All = all censuses combined, n = number of censuses.

Common name	Scientific name	All $n = 194$	1–30 Nov $n = 52$	1–30 Dec $n = 42$	31 Dec–29 Jan $n = 46$	30 Jan–28 Feb $n = 54$
Northern Flicker	*Colaptes auratus*	171	0.962 A	0.986 A	0.873 AB	0.768 B
American Tree Sparrow	*Spizella arborea*	157	0.562 B	0.958 A	0.962 A	0.857 A
Tufted Titmouse	*Baeolophus bicolor*	153	0.673 B	0.642 B	0.902 A	0.929 A
Red-winged Blackbird	*Agelaius phoeniceus*	143	0.926 A	0.626 BC	0.579 C	0.831 AB
Western Meadowlark	*Sturnella neglecta*	99	0.576 AB	0.318 C	0.396 BC	0.737 A
Golden-crowned Kinglet	*Regulus satrapa*	84	0.604 A	0.669 A	0.321 B	0.127 B
Northern Bobwhite	*Colinus virginianus*	66	0.382 AB	0.461 A	0.364 AB	0.211 B
White-crowned Sparrow	*Zonotrichia leucophrys*	36	0.385 A	0.095 B	0.143 B	0.157 B
Ring-necked Pheasant	*Phasianus colchicus*	34	0.240 A	0.183 AB	0.014 B	0.294 A
Common Grackle	*Quiscalus quiscula*	24	0.308 A	0.060 B	0.024 B	0.071 B
Eastern Meadowlark	*Sturnella magna*	20	0.070 B	0.018 B	0.089 B	0.205 A
Field Sparrow	*Spizella pusilla*	18	0.270 A	0.071 B	0.056 B	0.032 B
White-throated Sparrow	*Zonotrichia albicollis*	14	0.173 A	0.060 AB	0.018 B	0.018 B
Lincoln's Sparrow	*Melospiza lincolnii*	13	0.130 A	0.065 AB	0.000 B	0.050 AB

American Crow (*Corvus brachyrhynchos*) 194, Black-capped Chickadee (*Poecile atricapillus*) 194, Dark-eyed Junco (*Junco hyemalis*) 193, Northern Cardinal (*Cardinolis cardinalis*) 192, House Sparrow (*Passer domesticus*) 192, Blue Jay (*Cyonocitta cristota*) 190, American Goldfinch (*Carduelis tristis*) 187, White-breasted Nuthatch (*Sitta carolinensis*) 187, Red-bellied Woodpecker (*Melanerpes carolinus*) 184, Downy Woodpecker (*Picoides pubescens*) 170, European Starling (*Sturnus vulgaris*) 169, American Robin (*Turdus migratorius*) 167, Red-tailed Hawk (*Buteo jamaicensis*) 157, Hairy Woodpecker (*Picoides villosus*) 143, Harris's Sparrow (*Zonotrichia querula*) 136, Eastern Bluebird (*Sialia sialis*) 128, Carolina Wren (*Thryothorus ludovicianus*) 97, Red-headed Woodpecker (*Melanerpes erythrocephalus*) 92, Rock Dove (*Columba livia*) 81, Song Sparrow (*Melospiza melodia*) 68, American Kestrel (*Falco sparverius*) 49, Brown Creeper (*Certhia americana*) 47, Northern Harrier (*Circus cyaneus*) 41, Cedar Waxwing (*Bombycilla cedrorum*) 40, Bewick's Wren (*Thryomanes bewickii*) 36, Spotted Towhee (*Pipilo maculatus*) 33, Wild Turkey (*Meleagris gollopavo*) 29, Mourning Dove (*Zenaido mocroura*) 27, Pine Siskin (*Corduelis pinus*) 23, Brown-headed Cowbird (*Molothrus ater*) 20, Yellow-bellied Sapsucker (*Sphyrapicus varius*) 16, Winter Wren (*Troglodytes troglodytes*) 16, Sharp-shinned Hawk (*Accipiter striatus*) 14, Yellow-rumped Warbler (*Dendroico coronato*) 11, Loggerhead Shrike (*Lanius ludovicianus*) 7, Rough-legged Hawk (*Buteo lagopus*) 6, Horned Lark (*Eremophila olpestris*) 6, Rusty Blackbird (*Euphagus carolinus*) 6, Cooper's Hawk (*Accipiter cooperii*) 4, Purple Finch (*Carpodacus purpureus*) 3, Prairie Falcon (*Falco mexicanus*) 3, Fox Sparrow (*Passerella iliaca*) 3, Sedge Wren (*Cistothorus platensis*) 2, Red-breasted Nuthatch (*Sitta canadensis*) 2, Brown Thrasher (*Toxostoma rufum*) 2, Hermit Thrush (*Cathorus guttatus*) 1, Yellow-headed Blackbird (*Xanthocephalus xanthocephalus*) 1.

Short Communications

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Possible Winter Quarters of the Aleutian Tern?

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ABSTRACT.—Recent observations of the Aleutian Tern (*Sterna aleutica*) in the coastal waters around Hong Kong in spring and fall, and Singapore and the Indonesian islands of Karimun and Bintan between October and April indicate that at least part of the population of this species migrates through and winters in these areas. Our observations during December 1997, suggest that the coastal waters of Java, Bali and Sulawesi may form an additional part of the winter range of this species. *Received 3 August 1998, accepted 17 June 1999.*

The Aleutian Tern (*Sterna aleutica*) breeds along the western coast of Alaska (USA) and in Asia on the east coast of Kamchatka and Sakhalin (American Ornithologists' Union 1998). In Alaska, birds return to colonies during early May and then disperse during August and September after breeding, (Harrison 1983). Both the AOU Checklist (1998) and Harrison (1983) state that this species' winter range is "unknown".

During the last decade or so there has been a steady accumulation of records for this species outside its breeding range from Southeast Asia. Lee (1992) reported six specimens collected in May 1984 in the Mindanao Sea off Bohol, Philippines. Brazil (1991) noted approximately ten records from Honshu and Hokkaido, Japan including one instance of probable breeding. One exceptional record involves the occurrence of a single vagrant bird on the Farne Islands off the coast of northeast England during May 1979 (Dixey et al. 1981). More recently, during August and September 1992 as many as 190 birds were observed off the southern and southeastern coast of Hong Kong (Kennerley et al. 1993).

Initially birds were observed in breeding (alternate) plumage in late August but most then molted into non-breeding (basic) plumage during September. Details of the latter, poorly known plumage, can be found in Lee (1992), Kennerley and coworkers (1993) and Kennerley and Ollington (1998). Subsequently, small numbers have been observed annually in Hong Kong waters including individuals in breeding plumage during April–June. It is now established there as a regular and fairly common migrant in varying numbers. Several hundred migrants have also been recorded annually in August and September, with occasional birds recorded in October (Leven et al. 1994; Carey et al. 1995, 1996).

From September to October 1994 this species was common within the Riau Archipelago, Indonesia, and a single bird was also recorded there in March 1996 (Rajathurai 1996). Kennerley and Ollington (1998) observed small numbers between 18 September and 25 April in the Straits of Malacca and in the seas around the island of Grand Karimun with a maximum number of 15 positively identified birds on 19 January 1996, with more than 100 distant terns also present.

Small numbers of Aleutian Terns were also observed off the east coast of Singapore in September and October 1994 (Kennerley and Ollington 1998). No records were reported during 1995 but a concerted effort to locate this species in 1996 resulted in at least 15 birds sighted 13 October in the Straits of Singapore between Jurong and the Horsburgh Light (Kennerley and Ollington 1998).

We report here the first probable records from Java, Bali, and Sulawesi in the Republic of Indonesia and identify a likely proportion of this species' wintering range.

On 30 November 1997 between Labuan and the north coast of Ujung Kulon National Park, at the western tip of Java, from a boat we observed, about 20 probable adult Aleutian Terns in groups of 3–6, all in non-breed-

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ing plumage. We obtained good views of these birds in flight and perched as they fished together with other seabirds among and from the numerous fish-trap platforms. Similarly, on 4 December 1997 we also observed, from a boat a flock of approximately 35 probable Aleutian Terns during the late afternoon. They were feeding just off the west coast of Bali, within the maritime boundary of Bali Barat National Park. On 13 December 1997 we observed a group of 15 probable Aleutian Terns and Crested Terns (*Sterna bergii*) fishing at the mouth of the Bone River, Gorontalo, Sulawesi. At the same time, about 200 unidentified terns were feeding offshore along the interface between the muddy river water and the clear sea.

We observed the flocks closely for 10–30 minutes, as two of the flocks of the birds often fed close to our boat. N.P.H. is familiar with the species on its breeding grounds and has observed it twice in Alaska and once in Siberia. Both of us are familiar with the black-billed race of Common Tern (*Sterna hirundo longipennis*), which the Aleutian Tern most resembles. All the birds we saw appeared to be adults in winter or near winter plumage with a sharply defined pattern of extensive white forehead, with white extending onto the crown of some individuals creating a bald-headed appearance. Some individuals had a black nape with whitish streaking in the upper edge of the black nape (for an example see photographs 6 and 10 in Kennerley and Ollington 1998). The wings and back were dark grey with a contrasting pale rump and tail. The bill was black on all the birds as were the legs of perched birds off the west coast of Java. Flight appeared to be slower than that of a Common Tern and feeding was accomplished more by dipping, similar to *Chlidonias* terns or the tropical Sooty and Bridled terns (*S. fuscata* and *S. anaethetus*). Unfortunately we did not take note of the underwing pattern which Kennerley and Ollington (1998) and Kennerley (pers. comm.) demonstrate to be a diagnostic field identification character for the Aleutian Tern in winter plumage.

While our records of the Aleutian Tern in Java, Bali and Sulawesi are not conclusive, we have presented our records here in order to draw attention to a possible wintering area for this species and to encourage field workers visiting Southeast Asia and Wallacea to be more diligent in their examination of tern flocks, especially from September to April. Our records of a probable Aleutian Tern in Indonesia together with previously published observations of this species elsewhere in Southeast Asia suggest that a significant proportion of the western Pacific population of Aleutian Tern migrates along the southern coast of China and Southeast Asia to winter in the islands of Indonesia and possibly the Philippines.

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Arthropods and Predation of Artificial Nests in the Bahamas: Implications for Subtropical Avifauna

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ABSTRACT.—Little is known of nest predation patterns in the dry subtropics. We used artificial nests to examine patterns of nest predation and to identify possible nest predators in the Bahamas. Unlike predation patterns in temperate areas, we found no relationship between predation rates and nest cover or distance to the road. Instead, the rate of nest predation depended on distance to ocean. This result and a photograph taken at a disturbed nest implicated the giant white land crab (*Cardisoma guanhumi*) as a possible nest predator. Because land crabs are prevalent throughout the subtropics and could potentially influence nesting behavior, we advise researchers to consider variables associated with land crabs when examining nest predation in the subtropics. *Received 14 July 1998, accepted 15 April 1999.*

Nest predation studies are abundant in the literature; most have been conducted in northern, temperate areas (reviewed by Paton 1994, Major and Kendal 1996, Hartley and Hunter 1998). Although a few similar studies have taken place in the tropics (e.g., Gibbs 1991, Laurance et al. 1993) and wet subtropics (Latta et al. 1995), no such study has been conducted in dry, subtropical habitat where predator species assemblages may be quite different. Patterns of nest predation might differ in the dry subtropics as a result of differences in numbers and species of egg predators.

Long Island, an outer island in the southern Bahamas archipelago, is characterized by dry, scrubby vegetation and a relatively depauperate fauna. There has been no prior study to examine avian nest predation on any of the Bahama islands or to determine which egg predators are present. We used artificial nests to determine factors influencing nest survival of ground-nesting birds and to identify important nest predators on Long Island and Hog Cay, Bahamas. Artificial nests are frequently used in predation experiments where it is assumed that they provide a reasonable assessment of the impact of predators on real nests (Burger et al. 1994, but see Major and Kendal 1996). In temperate zone studies, nest predation rates often varied with nest visibility (Major and Kendal 1996) and distance from edge (Paton 1994). We conducted an experiment to determine whether patterns of nest predation in the Bahamas were similar to those observed elsewhere and to identify possible nest predators.

STUDY AREA AND METHODS

We conducted our study on the northern 20 km of Long Island and on Hog Cay, Bahamas. Long Island, one of the outer islands of the Bahamas archipelago, is 128 km long and 6.4 km wide at its widest point. Hog Cay is a small (100 ha), privately owned island located off the northern tip of Long Island. Both islands are covered with dry, scrubby vegetation. Mangroves (*Rhizophora mangle* and *Avicennia germinans*) grow along the coasts of both islands.

We observed 7 ground nesting bird species on Long Island and Hog Cay, Bahamas. The largest included the West Indian Whistling-duck (*Dendrocygna arborea*) and White-cheeked Pintail (*Anas bahamensis bahamensis*). Smaller species included Antillean Nighthawks (*Chordeiles minor*), Common Ground-Doves (*Columbigallina passerina*), Snowy and Wilson's plovers (*Charadrius alexandrinus* and *C. wilsonia*), and Willets (*Catoptrophorus semipalmatus*).

Potential terrestrial nest predators included introduced rats (*Rattus* spp.), domestic dogs (*Canis familiaris*), and native giant white land crabs (*Cardisoma guanhumi*). Possible avian egg predators included Laughing Gulls (*Larus atricilla*), Yellow-crowned

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Night-Herons (*Nyctanassa violacea*), and Smooth-billed Anis (*Crotophaga ani*).

We utilized artificial ground nests in two experimental trials lasting from mid-May through July 1995. Each trial was 30 days, the approximate incubation time for several ground nesting species in the Bahamas (Paterson 1972). For each trial, two plots were selected on Long Island and one plot was selected in similar habitat on Hog Cay. Trial 1 took place May 17–June 19 and consisted of 25 and 16 nests on Long Island, and 30 nests on Hog Cay. Trial 2 took place June 20–July 21 and consisted of 24 and 16 nests on Long Island, and 30 nests on Hog Cay. Artificial nests were placed in a grid pattern within each of the six sites such that one edge of the grid was located parallel to and 50 m from a road. All nests within the grid were placed 25 m apart and were randomly assigned as "hidden" or "open." Hidden nests were completely covered by vegetation, whereas open nests could be seen from within 1 m.

Nests consisted of a shallow scrape containing five domestic chicken eggs located under thatch palm (*Thrinax microcarpa*) or a dense bush. Although some studies have detected effects of egg size because small predators (e.g., mice) were unable to break larger eggs (Picman 1988, Haskell 1995), we believe that all potential predators in our study sites were large enough to handle chicken eggs. Nests were examined for survivorship at days 6, 12, 18, and 24, and were considered depredated if one or more eggs was missing or damaged.

To identify specific nest predators, we placed three automatic cameras with flash capability at one nest on each study site during each trial. Cameras were triggered by a motion-sensitive mercury switch glued to the bottom of the eggs. Because cameras were conspicuous, they were placed at previously depredated nests, which were then rebaited with chicken eggs. Cameras were rotated among nests within study sites on a weekly basis.

We also noted the remnants of eggs at the first predation event for each nest. Predators can sometimes be identified by the type of egg remains they leave behind (Reardon 1951; but see Trevor et al. 1991). Depredated eggs were classified as missing or broken (portion of an egg remaining in nest), and appearance of broken eggs was also noted (e.g., many small fragments, half shell remaining).

We developed a logistic regression model to examine the dependency of nest fate on nest type (i.e., hidden or open), distance to road (to examine edge effects), and distance to the ocean (a variable associated with land crab presence). Logistic regression models have been used to analyze factors affecting the success of both natural (Thomas et al. 1996) and artificial nests (Burger et al. 1994, Vander Haegen and DeGraaf 1996) and are appropriate when response variables are binary (e.g., nest success or failure) and factors are continuous (e.g., distance to road/ocean; Hosmer and Lemeshow 1989). We determined the suitability of the model by using the Hosmer and Lemeshow Goodness-of-Fit Test and associated statistic with a significance level of $P < 0.05$. Individual variables within the model were tested with the Wald χ^2 statistic. Analyses were conducted with SAS (Windows version 6.12; SAS Institute Inc., Cary, North Carolina).

RESULTS

Of 141 artificial nests, 99 (70%) were depredated during the two trials combined. Our overall regression model fit our data (Hosmer and Lemeshow Goodness-of-Fit statistic = 8.57, df = 8, $P = 0.38$) and was significant (score statistic = 21.73, df = 3, $P < 0.001$). Nest fate depended primarily on distance to the ocean (score statistic = 16.4, df = 1, $P < 0.001$). Nests ranged from 100–1500 m from the ocean; the probability of nest success increased with distance from the ocean. Nests located farthest from the ocean (1500 m) had the greatest success (71%), whereas those located 100–325 m from the ocean and had an average success rate of 23% (range 7–37%).

Nest fate was independent of nest type (hidden or open; $\chi^2 = 2.56$, df = 1, $P > 0.05$); 44 (63%) and 54 (76%) of the nests were disturbed at hidden and open nests, respectively. In addition, nest fate was not associated with distance to roads ($\chi^2 = 0.18$, df = 1, $P > 0.05$).

One camera successfully captured activity near a nest. A photograph was taken of a giant white land crab near two damaged eggs in a nest on Hog Cay. It was not clear whether the crab broke the eggs, or found them after they had been broken.

Of the 190 eggs from 92 nests on which data were collected, 73 (38%) were missing and 117 (62%) were broken at the first nest check after predation. Thirteen (12.5%) of the broken eggs were attributed to rat predation (Flack and Lloyd 1976, pers. obs.).

DISCUSSION

Although the results of artificial nest experiments conducted in the temperate zone are often inconsistent, a few common patterns have emerged. In general, predation rates are higher in nests that are more visible and in habitats with little understory cover (Major and Kendal 1996, Hartley and Hunter 1998). In addition, Paton (1994) found a negative relationship between nest predation rates and distance from habitat edge in most of the 14

artificial nest studies he re-analyzed. We found no such patterns in the Bahamas.

In our study, the only environmental variable that successfully predicted nest fate was distance to the ocean, suggesting that nests were depredated by a species residing in or near the water. Our photograph of a giant white land crab at a nest suggests that land crabs were depredating artificial nests.

Although land crabs are terrestrial and do not rely on the ocean directly on a daily basis, they do need some source of water nearby to survive and the females migrate to the ocean for reproduction to release larvae (Wolcott 1988). Given their reliance on water for reproduction and oxygen exchange, land crabs are generally limited to low-lying areas near mangroves, swamps, and streams, and are rarely more than a few kilometers from the sea (Wolcott 1988).

Giant white land crabs were abundant on both Hog Cay and Long Island but did not appear to be associated with edge habitats. Their mostly vegetarian diets and ground foraging habits could bring them into contact with ground nests regardless of whether the nests were hidden or open. Experiments involving captive land crabs revealed that crabs were able to crack and consume eggs of various sizes corresponding to the egg sizes of ground nesting birds in the Bahamas (Staus and Barnwell 1996). This study also indicated that crabs could be responsible for both broken and missing eggs.

Although some studies document chick predation by giant white land crabs (Gnam 1991), ours is the first study to implicate *Cardisoma* crabs as egg predators. Egg eating behavior has been documented in several *Gecarcinus* spp., land crabs in the same family as *C. guanhumi* (Rockwell 1932, Atkinson 1985, Burger and Gochfeld 1988, Burger et al. 1989). Other egg eating species include hermit crabs (*Coenobita rugosa*; Atkinson 1985, Burger et al. 1989), coconut crabs (*Birgus latro*; Atkinson 1985), and ghost crabs (*Ocypode quadrata*; Watts and Bradshaw 1995).

It has been suggested that land crabs play an ecological role similar to that of rats, and that crabs may have exerted considerable influence on tropical island avifuanas (Atkinson 1985). For example, after examining the fossil record, Olson (1981) hypothesized that *Gecarcinus* land crabs in the South Atlantic may have prevented the colonization of some islands by burrowing and ground-nesting petrels. Burger and Gochfeld (1988) provided evidence that Roseate Terns (*Sterna dougallii*) in Puerto Rico chose nest sites far from suitable land crab (*G. ruricola*) habitat. The widely distributed giant white land crab might have a similar effect on bird populations within its range.

Our results suggest that egg predation patterns and predator species assemblages in the dry subtropics may be different than those in northern temperate areas. Specifically, land crabs may play a significant role as egg predators. In the future, we urge researchers to consider environmental variables associated with the presence of land crabs (e.g., density of crab burrows, altitude, distance from ocean) when examining nest predation in the subtropics.

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Notes About the Distribution of *Pauxi pauxi* and *Aburria aburri* in Venezuela

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ABSTRACT.—In this paper I review the current distribution of the Northern Helmeted Curassow (*Pauxi pauxi*) and the Wattled Guan (*Aburria aburri*) in Venezuela. The historical range of *P. pauxi* was reduced as a result of human population growth and habitat perturbations. The current distribution corresponds principally with 18 national parks located from the northern coastal mountains of central Venezuela to the Andes Cordillera and Sierra de Perijá. *Pauxi pauxi* was recorded only in three localities outside national parks and may have expanded from its historical distribution in the eastern part of the country. *Aburria aburri* was recorded in Sierra de Perijá and western Mérida to southern Táchira, including four new localities; three in national parks. Both species are endangered in Venezuela and their survival will depend on environmental education programs and enforcement of the law. *Received 9 Feb. 1998, accepted 20 July 1999.*

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The Wildlife Conservation Society of the New York Zoological Society funded a study on human impacts on game species in protected areas of Venezuela from 1985 to 1990 (Silva and Strahl 1991, 1994, 1996, 1997). During 1985–1996, censuses and interviews were conducted and new data about the distribution of *Pauxi pauxi* (Northern Helmeted Curassow) and *Aburria aburri* (Wattled Guan) were collected. My objective in this paper is to present these data and review the status of *P. pauxi* and *A. aburri* in Venezuela.

In Venezuela *Pauxi pauxi* ranges from the northern coastal mountains of central Venezuela to the Andes Cordillera and Sierra de Perijá in rain forest and cloud forest. Most authors (Wetmore and Phelps 1943; Phelps and Phelps 1958, 1962; Delacour and Amadon 1973; Meyer de Schauensee and Phelps 1978; Collar et al. 1992; Rodriguez and Rojas-Suarez 1995) cited the states and localities of the historical range as follows: *P. p. pauxi*: southern Miranda state in Cerro Negro (Guatopo National Park); north Caracas in El Calvario; Distrito Federal; coastal mountains in Aragua state (Henri Pittier National Park); Carabobo state in Valencia, San Esteban, and Montalbán; east Falcón to Yaracuy state in Tucacas, Nirgua, mountains inland from Aroa, and Lagunita de Aroa; Lara state in Cubiro, and Yacambú National Park; from northern Mérida to southern Táchira state in Montaña de Limones, La Azulita, and Burgua. *Pauxi p. gilliardi*: Zulia state from southern Sierra de Perijá (Sierra de los Motilones) to southern Rio Tucuco, in Fila Macoíta, Campamento Avispa, Cerro Yin-taina, upper Río Negro, and La Sabana. A continuous distribution in the historical range was assumed (Fig. 1A) because of historical records, and Central Cordillera and Los Andes Cordillera were almost a continuous forest in the past.

The habitat available for *P. pauxi* has been greatly reduced as a result of deforestation, fragmentation, and habitat alteration. Almost all the remnant forest available in northern Venezuela was decreed as national parks by the Venezuelan government. Consequently, these national parks are isolated. I found that the current distribution of *P. pauxi* mainly coincided with the distribution of national parks situated in its historical range (Fig. 1B), as well as new localities such as Sierra de San Luis, Cueva Quebrada del Toro, and Tirgua National Parks. Although it was reported in Morrocoy National Park (Collar et al. 1992, Wege and Long 1993), according to the rangers, it was no longer present in the park in 1996.

Pauxi pauxi is rare in national parks and almost extinct outside national parks because hunting pressure is highest outside the parks (Silva and Strahl 1991, 1996, 1997). The few locations where *P. pauxi* was found outside national parks included the Sanchón River Hydraulic Reserve (10° 24′ N, 68° 09′ W), the Cojedes River Protectoral High Basin (10° 24′ N, 68° 15′ W) and Finca El Jaguar (10° 26′ N, 68° 59′ W).

From interviews with hunters I found that *P. pauxi* probably existed or may still live in eastern Venezuela. A hunter in Teresén (Monagas State) narrated the size, color pattern, and helmeted color of this species, and imitated its booming song. He recognized the bird from a set of cracid pictures. *Pauxi pauxi* was seen in La Hormiga (9° 54′ N, 62° 58′ W), Caño Payanuco, Guarapiche Forest Reserve (Sucre and Monagas States) between 1968 and 1973. Because only 1 of 25 interviewed hunters in Teresén saw a *P. pauxi,* and saw it only once, this should not be interpreted as range extension. The nearest locality of the historical distribution (Guatopo National Park) is approximately 405 km from Guarapiche Forest Reserve, and this separation is settled with towns and cities. More likely the former distribution record was incomplete. *Pauxi pauxi* is very likely to be extinct in Guarapiche because of high hunting pressure.

An interesting characteristic of *P. pauxi* is the brown phenotype that sometimes occurs in females. Males and females are typically black with a white belly. Hunters call the brown morph "Canaguey" or "Paují Amarillo." It was reported in the Sierra de Perijá, where two specimens were collected between 1941 and 1957 (Delacour and Amadon 1973). Here I report 26 new localities of the brown morph seen between 1949 and 1993 (Table 1). Of the 34 birds sighted, a single brown phenotype was seen with one black phenotype at Fila Real (1975), one with two black phenotypes at Casa de Tejas (1980), and one with seven black phenotypes at El Corazón (1988). Two brown phenotypes were seen with two

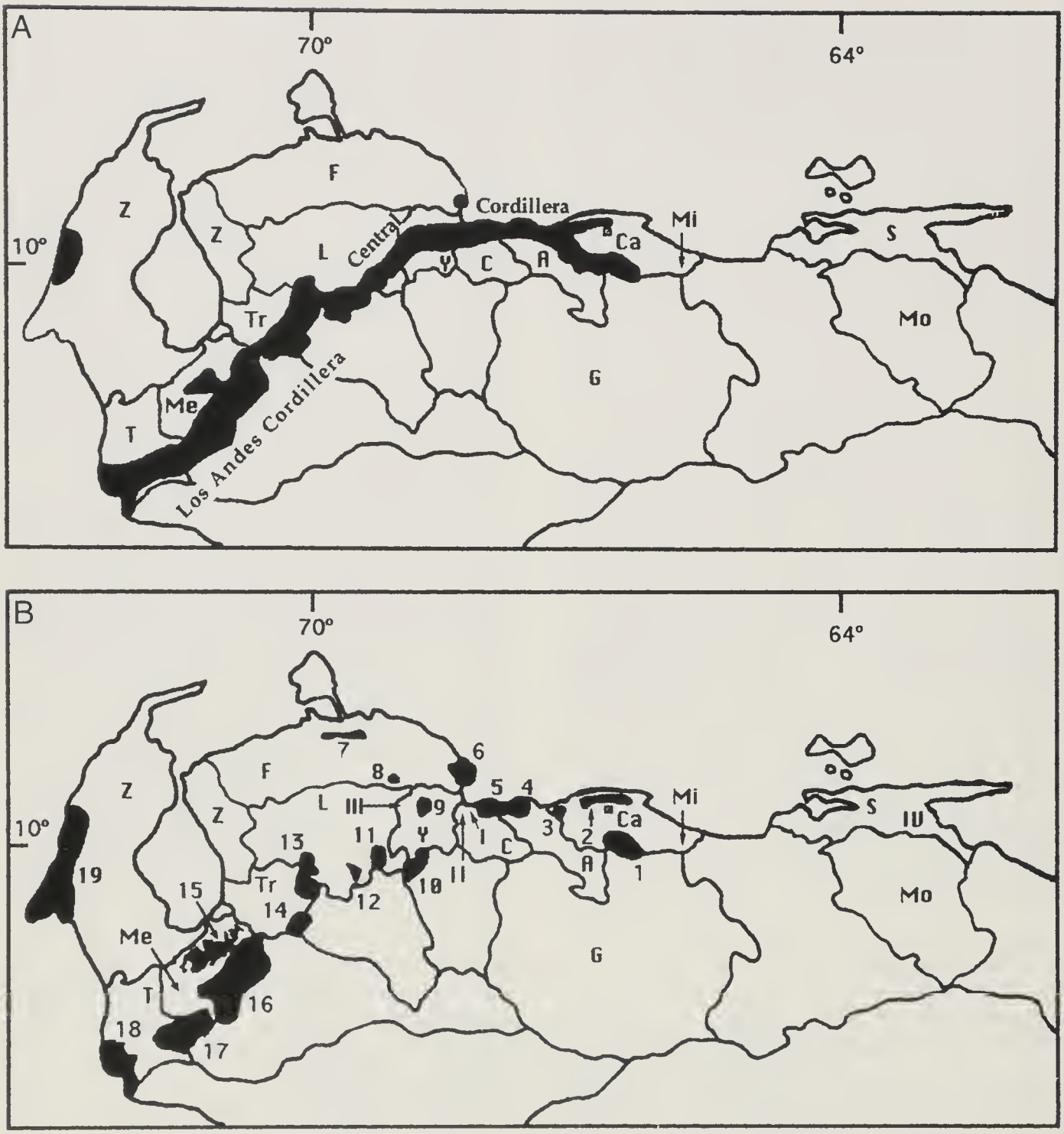

FIG. 1. A. Historical range of *Pauxi pauxi* according to Delacour and Amadon (1973), Meyer de Schauensee and Phelps (1978), Collar and coworkers (1992), and Rodriguez and Rojas-Suarez (1995). B. Current range of *Pauxi pauxi* in Venezuela. Boundaries of national parks are shown, but the species may not be distributed through the entire park. Numbers are national parks, Roman numerals are other localities, and letters are states with the exception of Caracas (Ca), the capital of Venezuela. Code: 1 = Guatopo (122,464 ha). 2 = El Avila (81,800 ha). 3 = Macarao (15,000 ha). 4 = Henri Pittier (107,800 ha). 5 = San Esteban (43,500 ha). 6 = Morrocoy (32,090 ha). 7 = Sierra de San Luis (20,000 ha). 8 = Cueva Quebrada del Toro (4,885 ha). 9 = Yurubí (23,670 ha). 10 = Tirgua. 11 = Terepaima (18,650 ha). 12 = Yacambú (14,580 ha). 13 = Dinira (42,000 ha). 14 = Guaramacal (21,000 ha). 15 = Sierra de La Culata (200,400 ha). 16 = Sierra Nevada (276,446 ha). 17 = Tapo—Caparo. 18 = El Tamá (109,000 ha). 19 = Sierra de Perijá (295,288 ha). I = Sanchón River Hidraulic Reserve (8,100 ha). II = Cojedes River Protectoral High Basin (276,000 ha). III = Finca El Jaguar (16,000 ha). IV = Guarapiche Forest Reserve (576,500 ha). Mo = Monagas. S = Sucre. G = Guárico. Mi = Miranda. Ca = Caracas. A = Aragua. C = Carabobo. Y = Yaracuy. F = Falcón. L = Lara. Tr = Trujillo. Me = Mérida. T = Táchira. Z = Zulia.

TABLE 1. Brown phenotype of *Pauxi pauxi* recorded in Venezuela.

Locality	Date	Location	Coordinates	*n*
Henri Pittier	1975	La Glorieta	10° 28′N 67° 45′W	1
Henri Pittier	03/1984	La Regresiva	10° 22′N 67° 44′W	1
Henri Pittier	1993	El Saltico	—[a]	2
Henri Pittier	1993	Los Riitos	—	2
San Esteban	1955	Burro Sin Cabezas	—	1
San Esteban	1960	Burro Sin Cabezas	—	1
San Esteban	1986–87	Flor Amarillo	—	1
San Esteban	1987	Flor Amarillo	—	1
San Esteban	07/1989	El Tanque	—	1
San Esteban	1991	San Felipe	—	1
San Esteban	?	El Dique	10° 18′N 67° 59′W	1
San Esteban	?	La Panta (Qda. Yaguas)	—	1
San Esteban	?	Ranchitos	—	2
San Esteban	?	La Manguera	—	2
Terepaima	1949	Los Portones	9° 52′N 69° 20′W	1
Terepaima	1975	Fila Real	9° 55′N 69° 16′W	1
Terepaima	04/1992	Fila Real	9° 53′N 69° 17′W	1
Yacambú	1979	El Blanquito, Qda. La Toma	9° 42′N 69° 34′W	1
Yacambú	1983	Barro Amarillo	—	1
Yacambú	1988	El Corazón	—	1
Yacambú	1988	La Cañada	—	1
Yacambú	06/1992	El Blanquito	9° 42′N 69° 34′W	1
Yacambú	?	La Escalera	9° 42′N 69° 30′W	1
Yacambú	?	La Postora	9° 41′N 69° 37′W	1
Yacambú	?	El Blanquito	9° 42′N 69° 34′W	1
Yacambú	?	Cerro Blanco	9° 37′N 69° 30′W	1
Sierra Nevada	?	Alto de la Aguada	8° 37′N 70° 40′W	1
Sierra Nevada	?	San Benito	8° 40′N 70° 37′W	1
Rio Sanchón	1980	La Cumbre del Cacho	—	1
Rio Sanchón	11/1980	Casa de Tejas	—	1

[a] Name of localities do not appear on maps because they are local names used by hunters and the exact locations are unknown.

black phenotypes at El Saltico and Los Riitos in 1993.

Aburria aburri was mainly recorded in the western part of Venezuela (Fig. 2). The historical range was reported to be in the Sierra de Perijá and west Mérida to southern Táchira in rain and cloud forest (Delacour and Amadon 1973, Meyer de Schauensee and Phelps 1978, Rodriguez and Rojas-Suarez 1995). The current distribution of *A. aburri* indicates that the record of the historical range may have been incomplete. *Aburria aburri* was recorded in Sierra Nevada National Park (54 interviewed hunters), in Terepaima National Park (observed), and in Yacambú National Park and the basin of Yacambú River (S. Boher, pers. comm., and 338 interviewed hunters). These were new distribution records, but they did not suggest an extension of the historical range because hunters over 60 years old hunted *A. aburri* since they were young. Perhaps, the historical range was continuous. Although Rodriguez and Rojas-Suarez (1995) stated that *A. aburri* probably was found in the eastern part of Costa Cordillera, they did not mention the source of their information.

The present status of *P. pauxi* and *A. aburri* is worrisome. According to the population censuses (Silva and Strahl 1991, 1997) and the interviews (Silva and Strahl 1996), *P. pauxi* and *A. aburri* have very low densities with *A. aburri* being more rare than *P. pauxi*. Both species were considered Endangered by the Cracid Specialist Group (Strahl et al. 1994) and by researchers of a recent study in Venezuela (Rodriguez and Rojas-Suarez 1995). Habitat destruction and illegal hunting are the principal causes of the decline in population of both species, and their conservation will rely on hunter education (Silva and Pel-

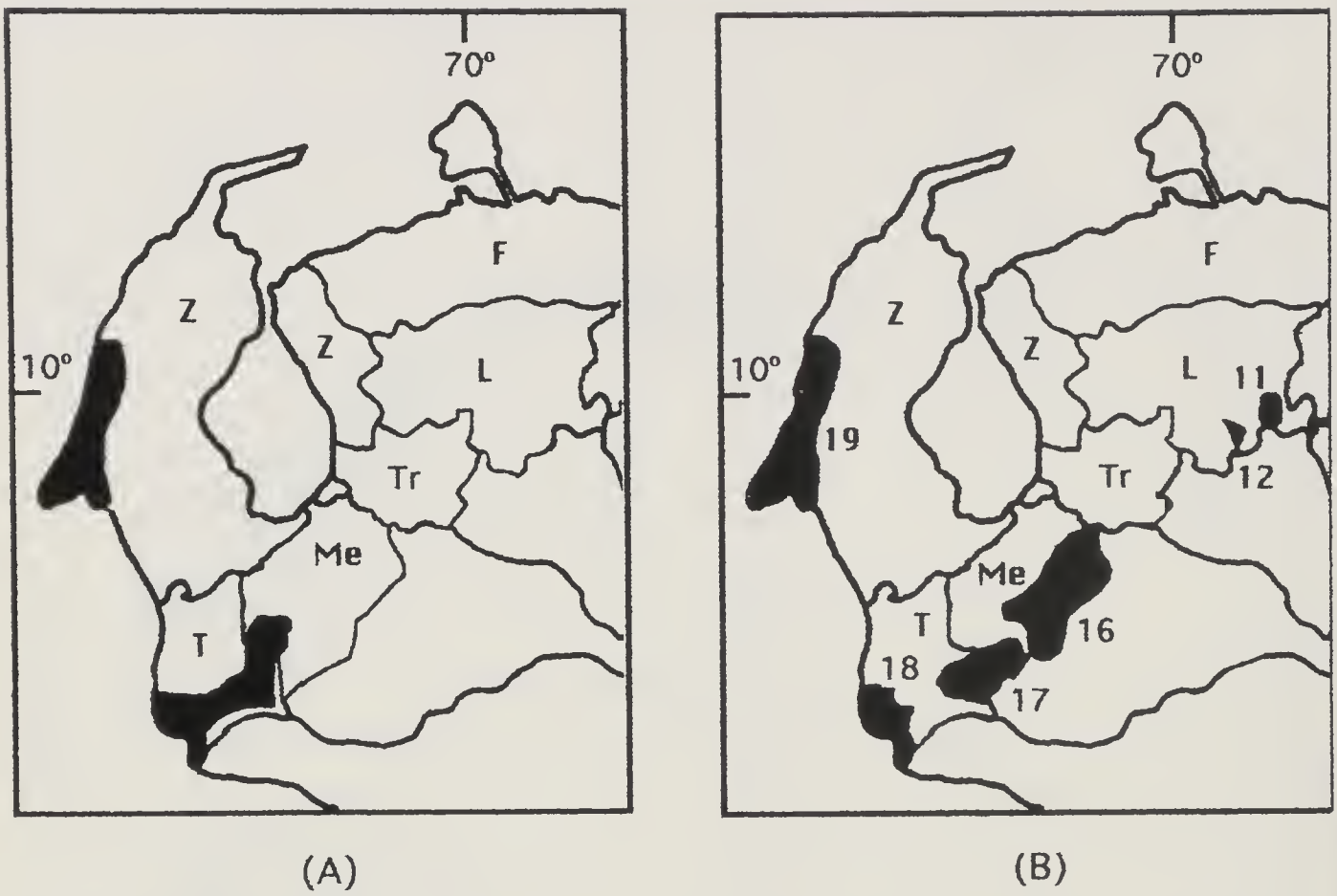

FIG. 2. Historical (A) and current distribution (B) of *Aburria aburri* in Venezuela. Abbreviations are the same as Fig. 1.

legrini 1996, Silva 1997) and enforcement of the law.

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Western Burrowing Owls in California Produce Second Broods of Chicks

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ABSTRACT.—We present the first evidence that western Burrowing Owls are capable of raising a second brood of chicks within a nesting season once their first brood successfully fledges. Two pairs of owls in central California known to have successfully fledged chicks from a first brood renested in 1998, with one pair producing five additional fledglings. *Received 29 March 1999, accepted 15 July 1999.*

Western Burrowing Owls (*Athene cunicularia*) are thought to be declining throughout much of their range (DeSante et al. 1997, James and Espie 1997). The potential causes of these declines vary with location, but likely include large-scale habitat destruction from farming or development, reductions in species such as ground squirrels that create the burrows that the owls use, and agricultural chemicals (James and Espie 1997, Gervais et al. in press). Because of the perceived threat to the viability of Burrowing Owl populations, the species has been listed as endangered, threatened, or of special management concern in a number of North American states and provinces (Haug et al. 1993).

Effective conservation at the species level requires understanding the population dynamics of the species in question, which in turn means accurate estimation of demographic parameters such as survival and reproductive rates. These can be used in simplified models that allow the examination of the effects of possible management actions or environmental perturbations on population persistence. Such an approach has recently been used for the northern Spotted Owl (*Strix occidentalis*; Noon and Biles 1990), and for predicting the effects of pesticide exposure on wildlife populations (Caswell 1996, Calow et al. 1997).

Simulations of generalized life history strategies have shown that for a species with relatively low adult survivorship and a short life span, reproductive success may be most influential in maintaining population viability (Emlen and Pikitch 1989). This is likely to be generally true for Burrowing Owls. They are capable of producing up to 12 eggs in a clutch (Haug et al. 1993), and we have observed up to 10 young fledged per nest in good reproductive years. In addition, Burrowing Owl annual adult survivorship appears to be quite low, with between-year return rates ranging from 33–58% (Haug et al. 1993), and a longevity record for a wild banded owl of 8 years and 8 months (Kennard 1975). If sensitivity analyses prove that the Burrowing Owl fits the predictions of the Emlen-Pikitch model (Emlen and Pikitch 1989) for a small, relatively short-lived species, then accurate assessment of reproductive potential of Burrowing Owls is essential to evaluating population processes.

Only Florida Burrowing Owls have been known to produce second broods within a season (Millsap and Bear 1990). We report two

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instances of western Burrowing Owl pairs attempting second broods after the first brood had successfully been fledged during the 1998 breeding season. To our knowledge, this is the first time the production of more than a single brood per season has been verified in western Burrowing Owls.

METHODS AND RESULTS

We have conducted demographic research since 1997 on a population of Burrowing Owls at Naval Air Station Lemoore (36° 20′ N, 119° 57′ W), 50 km southwest of Fresno, Californa. The naval air station supports approximately 65 breeding pairs of owls, which appear to be winter residents (Gervais and Rosenberg, unpubl. data). Nesting habitat on the station is primarily small patches of exotic annual grasses along runway easements and in wildlife areas surrounded by agricultural fields. Wildlife areas are fallow fields that are composed of exotic annual grasses and weeds, although they are burned annually. Approximately 75% of the adult resident population of owls is now banded with U.S. Fish and Wildlife Service bands and unique alpha-numeric rivet bands (Acraft Bird Bands, Edmonton, Alberta, Canada).

Early in the season, we collected eggs for use in an ongoing toxicology study (Gervais et al. in press). One sampled burrow contained at least four eggs and the incubating female on 19 April 1998. At that time, we identified the female from her bands and we removed one egg. Her mate also was previously banded and was identified by resighting his bands early in the nesting season. This nest successfully fledged two chicks in early June. We recaptured the female owl on 14 June using a mouse baited spring net. At capture, she weighed 198 g, well above the 150 g average for this species (Haug et al. 1993), and was noticeably swollen in the lower abdomen. Her brood patch was well developed and vascularized, suggesting nesting activity.

To verify that this female was indeed relaying, we used an infrared burrow probe (Christensen Designs, Manteca, California) to examine the burrow on 16 June. We observed the two fledged chicks in the entrance to the nesting chamber, but were unable to see beyond them. The burrow entrance had fresh decorations of coyote dung and the nest tunnel was lined with similar debris. The adults were observed at the burrow entrance throughout the next few weeks; individual identity was confirmed using their color bands.

We examined the nest again on 27 June, and observed four eggs in the nest chamber after the female flushed from the burrow entrance. We removed two eggs through an access hole originally dug for the toxicological study egg sampling (Gervais et al., in press). The eggs were cool, but the shells were very clean and candling revealed clear egg contents with no visible development. The eggs were returned to the nest after inspection and the access holes covered again with dirt and boards. We do not believe these eggs were from the previous nesting attempt because of their clear contents and clean shells. Eggs that sit in the burrow for eight weeks would have dark contents as they began to rot and shells would be covered with dirt and fecal matter from the chicks.

When we examined the burrow on 14 July, the eggs were gone. No owls were present at the burrow during that visit, although both adults continued to be sighted in the area through July.

A second double nesting attempt also occurred in 1998. We observed with the infrared burrow probe a banded female owl in her burrow with nine eggs on 16 April; she raised one chick to fledging after the disappearance of her mate. We observed this same female at the same burrow entrance in early September with five buffy breasted chicks. These chicks clearly had recently emerged from their burrows, because juvenile owls fledged during the main breeding attempt at this site have typically undergone a body molt by this time and their breasts are heavily streaked in the manner of adult birds. No other nests within the area still contained chicks at this time. The five chicks were frequently seen at the burrow entrance through the middle of September when fieldwork was discontinued. This is typical of young owls still fully dependent on their parents for food; owls fledged earlier in the season had dispersed from their natal burrows by early August as indicated by radio telemetry (Gervais and Rosenberg, unpubl. data). The owl's mate for this second attempt was also banded, but his bands were consistently too muddy to read and he was never identified.

Our fieldwork did not include detailed observations of all nests in our study area throughout the summer and early fall, but we did not find any other evidence in support of double brooding attempts. These attempts may be quite rare and only occur in exceptional years. The 1998 breeding season was marked by very late rains, resulting in a high proportion of renesting efforts by the owls (Rosenberg and Gervais, unpubl. data). The prolonged growing season that followed the wet spring may have led to conditions conducive to late-season breeding attempts, such as greater food availability.

Nevertheless, it is clear that at least in some conditions western Burrowing Owls can raise two broods of chicks, thus increasing their reproductive output. This may be important for individuals whose first broods were small because of predation or the loss of a mate, or for populations recovering from environmental damage such as pesticides or burrowing rodent control. This information is also important for use in sensitivity modeling such as that done by Emlen and Pikitch (1989) or Noon and Biles (1990), because accurate demographic parameter estimation is essential to determining life history strategies and evaluating demographic risks to populations.

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Continuous Nesting of Barn Owls in Illinois

Jeffery W. Walk,[1, 3] Terry L. Esker,[2] and Scott A. Simpson[2]

ABSTRACT.—Barn Owls (*Tyto alba*) typically begin nesting in temperate zones in early spring. The species has high reproductive output (large clutch size, occasionally double-brooded) and high mortality for a member of the Strigiformes. We report on Barn Owls in one nest box that hatched five clutches and fledged young from four clutches within 23 months. Laying, incubation, or brood-rearing was attempted in every month of the year. In the only clutch mortality we witnessed, three young apparently died of exposure during a period of cold weather (temperatures as low as −15° C). *Received 24 February 1999, accepted 27 May 1999.*

Barn Owls (*Tyto alba*) have a high reproductive rate and relatively short life span, fitting an *r*-selected life history strategy (Colvin et al. 1984, Marti 1997). Average clutch sizes in North America range from 4.2–7.1 eggs (mostly 5–6 eggs; Hands et al. 1989, Marti 1992) and the average Barn Owl life span is less than 2 years (1.4 years, Stewart 1952; 1.7 years, Keran 1981). Most nest initiations in temperate areas occur from February to June, with the peak probably occurring March–May (Hands et al. 1989, Marti 1992). Nestlings have been banded in every month except February in the northern United States (Stewart 1952), suggesting that nesting may occur in any season. Second broods are uncommon in temperate climates. For example, only about 5% of pairs in Utah produced a second brood (Marti 1992). In contrast, nesting in tropical areas occurs year around with double broods being common (e.g., Lenton 1984). In captivity, Maestrelli (1973) reported a pair fledging six broods in 22 months.

A nest box (enclosed design from Colvin 1983) was erected 4.6 m above ground in an empty barn in 1986. This location was within a 64 ha grassland tract of Prairie Ridge State Natural Area, Marion County, Illinois (38° 45′ N, 88° 51′ W). Prairie Ridge State Natural Area grasslands are a combination of restored native grasses and introduced cool-season grasses managed by the Illinois Department of Natural Resources for grassland wildlife. Within 2 km of the nest site, land use was about 70% rowcrop agriculture, 15% grasslands (96 ha of Prairie Ridge State Natural Area, 98 ha of Conservation Reserve Program grasslands), 8% small grains, and small amounts of woodland, pasture and farmsteads.

The nest box was checked periodically and Rock Dove (*Columba livia*) nests were removed. We first observed one adult Barn Owl perched upon the nest box on 20 September 1993. On 1 November 1993, two adults and a clutch of six eggs were noted. We saw three chicks on 21 December 1993 and found them dead in the nest box on 6 January 1994. The young apparently died of exposure to harsh weather between 23 and 31 December. Mean temperature during this period was −5.5° C (−15° to 3° C) with 7 cm snowfall on 25 December and northeasterly winds 20–25 km/hr blowing into the nest box on 28 and 29 December (weather data from Midwestern Climate Center, Champaign, Illinois). The second nest attempt began about 11 March 1994 (one egg in nest box), with five young seen through May 1994. Fledging occurred in early July (four grown birds observed 14 July). An adult and the third clutch of five eggs were noted 23 August 1994. Four chicks from this clutch fledged between 25 and 30 October. The fourth nest attempt was apparently initiated in early to mid-February 1995. A clutch of seven eggs was observed 13 March, and five young about to fledge were seen 9 May 1995. A fifth clutch consisted of three eggs recorded on 7 July 1995, three young (estimated two weeks old) on 23 August and two fledglings on 19 October 1995. Single Barn Owls were observed only sporadically after this date.

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The five clutches averaged 5.2 eggs per clutch (range 3–7). Of the four successful clutches, 3.75 young fledged per clutch (range 2–5). We estimate an average of 160 days (range 130–190 days) for each successful nest cycle (estimated time between the start of one attempt and the start of the next). While these birds were not banded or marked, their constant presence at the nesting site from September 1993 to October of 1995 suggests the same adults were involved in all nest attempts.

Excluding the first nest attempt, the temporal pattern of the four successful nests better fits the typical early spring/late summer pattern of double-brooded Barn Owls (Taylor 1994), although the 1995 nests were about one month earlier than their 1994 counterparts. Taken as a whole, this nest site was used nearly continuously for two years with an additional delay of about 30 days between nest attempts during the coldest time of year.

This is only the fourth report of Barn Owls using a nest box in Illinois (Illinois Biological and Conservation Data System, unpubl. data). Once this nest site was discovered, breeding activity was brief, but quite productive.

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Unusual Nest Sites for Southwestern Willow Flycatchers

Scott H. Stoleson[1,2] and Deborah M. Finch[1]

ABSTRACT.—The endangered southwestern Willow Flycatcher (*Empidonax traillii extimus*) is an obligate riparian species that typically nests in willow (*Salix* spp.) thickets or other dense, shrubby habitats. We report on the first nests in Arizona sycamore (*Platanus wrightii*) and in a climbing rose vine (*Rosa multiflora*). Although these nests were located in novel substrates, they were typical for the species in being supported by multiple small stems and in having a dense canopy cover. We suggest that nest substrate preferences of Willow Flycatchers in the Southwest may be broader than generally considered. *Received 17 Nov. 1998, accepted 6 March 1999.*

The southwestern Willow Flycatcher (*Empidonax traillii extimus*), a federally-listed endangered species, is an obligate riparian specialist that breeds in dense vegetation associated with watercourses (U.S. Fish and Wildlife Service 1995). Most studies of habitat preferences in Willow Flycatchers have shown a strong association with willow (*Salix* spp.) thickets or other shrubby habitats (McCabe 1991, Sedgwick and Knopf 1992). In the Southwest, nests of this subspecies have been found most commonly in willows, salt cedar (*Tamarix* spp.), and locally in forbs such as stinging nettles (*Urtica dioica holosericea*) or trees such as boxelder (*Acer negundo*), alder (*Alnus* spp.), Russian olive (*Eleagnus angustifolia*), and young Fremont cottonwoods (*Populus fremontii*; Sferra et al. 1997; Sogge et al. 1997). In this paper we report on the first recorded incidence of Willow Flycatchers nesting in Arizona sycamore (*Platanus wrightii*) and in a nonnative climbing rose (*Rosa multiflora*).

These observations were made as part of a study of southwestern Willow Flycatchers in the Gila River valley near the towns of Cliff and Gila, Grant County, New Mexico (32° 57′ N, 108° 35′ W). The study area consists of patches of riparian woodland along the river and earthen irrigation ditches at elevations averaging 1400 m. Most of the valley bottom is used for ranching and farming. Woodland patches are composed primarily of Fremont cottonwood, Goodding's willow (*Salix gooddingii*), boxelder, Arizona sycamore and Arizona walnut (*Juglans major*), with an understory of shrubs, forbs, and grasses. This valley supports the largest known population of Willow Flycatchers in the Southwest, with an estimated 230 pairs in 1998 (Stoleson and Finch, unpubl. data; P. Boucher, pers. comm.).

Nesting habits at this site differed from what has been reported elsewhere in the Southwest. Of 257 nests located in 1997–1998, 76.5% were placed in boxelder, 8.6% in willows, 6.3% in Russian olive, and the remainder (<5% each) in Arizona alder (*Alnus oblongifolia*), seepwillow (*Baccharis glutinosa*), Fremont cottonwood, salt cedar, Arizona sycamore, and rose.

One pair of Willow Flycatchers was found building a nest in a sycamore on 8 June at the Fort West Ditch site on the Gila National Forest (FS-4). This nest was too high for its contents to be visible (nest characteristics in Table 1). Parents were observed carrying food to the nest on 1 and 6 July. On 13 July, the parents were observed feeding at least two fledglings in the surrounding trees. This nest was in a cluster of five vertical twigs on a small branch. Although the nest tree was very open, the nest itself was immediately beneath a dense layer of foliage.

A second sycamore nest (GRP-7) was located in The Nature Conservancy of New Mexico's Gila Riparian Preserve on 23 July. The female was on the nest incubating or brooding. On 31 July the nest was found empty and disheveled, presumably the result of predation. This nest was located in a cluster of about 12 vertical twigs at the end of a short, broken branch. Like the previous nest, the nest was visible from the sides but covered from above by dense foliage.

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TABLE 1. Characteristics and outcomes of southwestern Willow Flycatcher nests in rose and sycamore in the Gila River valley, southwestern New Mexico, 1998.

	Nest characteristics							
Nest	Substrate	Nest ht. (m)	Canopy ht. at nest (m)	Canopy cover (%)[a]	Nest plant diameter (cm)[b]	Distance to water (cm)[c]	Distance to edge (m)[d]	Outcome
SE1-19	rose	3.5	13.9	94	0.7	8	33	fledged 2
FS-4	sycamore	13.6	17.9	94	33.0	31	10	fledged ≥2
GRP-7	sycamore	8.0	12.2	93	33.2	25	12	depredated

[a] Average percent canopy cover measured at base of nest plant and at points 4 and 8 m from base in four cardinal directions, measured using densiometers.
[b] Measured at 1.7 m above ground.
[c] Horizontal distance between base of nest plant and nearest perennial water.
[d] Defined here as horizontal distance between nest site and nearest area with no tree cover (i.e., shrubs, sand, or pasture).

On 18 June, an incubating bird was flushed from a nest in a rose vine climbing a large boxelder tree on the U-Bar Ranch (SE1–19). The nest contained two eggs at that time. On 13 July, two almost fully feathered fledglings were observed being fed in the undergrowth near the nest. The nest was placed at the junction of four stems of the nonnative *Rosa multiflora*, hanging from and about a meter below a leaning trunk of boxelder.

Willow Flycatcher nests have been found only rarely in native shrubby *Rosa* species in the Southwest, in California (W. Haas, pers. comm.) and at high elevations in Arizona (McCarthey et al. 1998). In the Palouse Hills of Washington, where Willow Flycatchers are not restricted to riparian habitats, rose was the most frequent nest substrate (King 1955). Similarly, 56% of nests in the interior of British Columbia were in rose (Campbell et al. 1997). Nests have been reported in rose elsewhere as well (Walkinshaw 1966; McCabe 1991; J. Sedgwick, pers. comm.).

Our observations emphasize that Willow Flycatchers are opportunistic in their choice of nesting substrates, apparently requiring only dense foliage and a suitable twig structure to support their nests (McCabe 1991, Sogge et al. 1997). Although the three nests reported here were unusual in terms of substrate species, they were very typical of flycatcher nests with respect to foliage density and twig structure (Table 1).

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Mortality of an Adult Veery Incurred During the Defense of Nestlings

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ABSTRACT.—Cost-benefit analyses of the adaptive significance of nest defense in birds are based on the assumption that parent birds attacking nest predators risk serious injury or death. However, there are few published records of adult birds dying during nest defense. I found an adult male Veery (*Catharus fuscesens*) dead in circumstances indicating that the bird died while defending his nest. This observation supports speculation that adult birds risk injury or death in the course of nest defense, and lends support to explanations of variability in nest-defense behavior that are presented in terms of cost-benefit analysis and the optimization of fitness. *Received 11 Jan. 1999, accepted 27 May 1999.*

On 27 June 1997 I located a Veery (*Catharus fuscesens*) nest containing 3 eggs 1.6 m from the ground in a 9 year-old clearcut in the White Mountain National Forest (43° 58′ N–70° 97′ W) in north-central New Hampshire. On 11 July I approached the nest and observed an adult on the rim of the nest with its tail tilted up in an unusual posture. The adult was dead, the body cold. Autopsy revealed that the adult was a male and that the body had numerous puncture wounds, one on the central-posterior region of the right pectoralis muscle and four more on the back in the vicinity of the synsacrum. The four puncture wounds on the back were symmetrically oriented on either side of the spine, 1.5–2.0 cm apart and up to 7 mm deep, and probably caused the death of the bird. The depth and spacing of the wounds suggest that the predator may have been a Sharp-shinned Hawk (*Accipiter striatus*), a species known to attack Veery nests (Day 1953).

The adult was missing all of its secondary feathers and all but three rectrices. The missing feathers were scattered over the nest and the immediate vicinity of the nest bush. Another adult, presumably the female, was heard alarm calling nearby. The nest cup was torn down and had come to rest on some branches of the nest bush below the original level of the nest. Two nestlings were found prone on ground beneath the nest. The nestlings were cold, and gaped weakly. Based on previous experience with the nesting phenology of this species, I estimated the nestlings to be at least three days short of fledging. The original clutch size was three eggs. It is unknown whether the third egg hatched. No sign of a third nestling or eggshells was found in the vicinity.

On the basis of several lines of evidence, I conclude the male Veery was killed in the course of nest defense. First, based on the spacing of the puncture marks, the predator was evidently large enough to consume a Veery (K. Doyle, pers. comm.). Under these circumstances, it is difficult to conceive of a scenario in which a predator would kill the adult, leave it on the nest, attempt to depredate the nest, and subsequently leave. In contrast, the disposition of the male, and of the nest and its contents are all consistent with the hypothesis that the adult was killed in association with nest defense. The adult was killed yet not consumed, indicating that it was not the original target of the predator. Furthermore, the nestlings were not consumed, suggesting that the predator was interrupted during the predation event. Veerys have been observed successfully defending nests by striking the predator with their wings (Nice 1962; Pettingill 1976, pers. obs.), which would account for the symmetrical loss of wing feathers I observed. It could be argued that the male was the original target of the predator, was wounded elsewhere, and returned to the nest seeking a secure hiding place, were it not for the fact that the nest had been attacked.

Cost-benefit analyses of the adaptive significance of nest defense in birds are based on the assumption that birds attacking predators during the course of nest defense are at some

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risk of injury or death (Montgomerie and Weatherhead 1988). However, observations of nest predation events under natural conditions are rare (Pettingill 1976) and observations of attacks on parent birds by predators during the course of nest predation are even more scarce. Brunton (1986) observed a Killdeer (*Charadrius vociferous*) killed by a red fox (*Vulpes vulpes*) while performing a distraction display. This observation of a Veery confronting a predator at the cost of its own life during active defense of the nest is to my knowledge, unprecedented. This observation supports speculation that adult birds assume risk of injury or death in the course of nest defense (Curio and Regelman 1985), and lends support to explanations of variability in nest-defense behavior that are couched in terms of cost-benefit analysis and the optimization of fitness (Montgomerie and Weatherhead 1988).

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Relationships of Clutch Size and Hatching Success to Age of Female Prothonotary Warblers

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ABSTRACT.—We obtained 1033 clutch sizes from 281 known-age female Prothonotary Warblers (*Protonotaria citrea*) nesting in nest boxes at Presquile National Wildlife Refuge in eastern Virginia from 1987 through 1998. Prothonotary Warblers typically nested twice during each breeding season; first clutches of all birds averaged 1.01 eggs greater than second clutches [4.96 ± 0.72 (SD) vs 3.94 ± 0.55]. Clutch size was significantly smaller in first nests of one-year-old warblers (4.64 ± 0.48) than in first clutches of females two to eight years old (5.05 ± 0.62). First clutches did not differ among age classes of birds older than one year. The mean size of second clutches was not significantly different among any of the age classes. One year old birds initiated laying significantly later than older birds (125.0 ± 6.4 vs 121.5 ± 7.7; Julian dates). The average number of infertile eggs in first clutches was larger in one year old females and differed significantly from that of older females (1.01 ± 0.90 vs 0.63 ± 0.87). The number of infertile eggs in second clutches did not differ significantly with female age. Significantly fewer eggs hatched in first nests of one year old birds than in those of older birds (3.75 ± 0.89 vs 4.33 ± 1.09). *Received 2 Dec. 1998, accepted 2 May 1999.*

The Prothonotary Warbler (*Protonotaria citrea*) is unusual among wood warblers (Parulidae) because it nests in secondary cavities. It shares this trait with only one other member of the 116 members of the subfamily Parulinae [Lucy's Warbler (*Vermivora luciae*); Curson et al. 1994]. It is likewise noteworthy among the birds of the eastern United States in that it migrates farther than the other small passerines nesting in secondary cavities. Determinants of clutch size of Prothonotary Warblers therefore may be of interest for comparison with other cavity-nesting passerines and with other Neotropical migrants. Several re-

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searchers have documented changes in reproductive success associated with age in cavity-nesting, passerine birds (Bryant 1988, McCleery and Perrins 1989, Sternberg 1989, Sæther 1990), but to date there have been few such data for a warbler.

Prothonotary Warblers are declining in the United States (Sauer et al. 1997), thus any knowledge of their demography may be useful in conservation of the species. In this paper we provide an analysis of a large set of measurements of reproductive performance of the Prothonotary Warbler that we have accumulated over the past 12 years. Specifically, we examine clutch size and infertility in this species and ask the question: Does clutch size and/or infertility of eggs change with age of females?

STUDY AREA AND METHODS

Our data were obtained from 1987–1998 in swamp forest along the James River near and on Presquile National Wildlife Refuge, Hopewell, Virginia (37° 20′ N, 77° 15′ W). The habitat of the study area is tidal swamp in which the dominant tree species are blaek gum (*Nyssa sylvatica*), red maple (*Acer rubrum*), and ash (*Fraxinus* sp.). These swamps have a relatively harsh environment where tree-surface temperatures regularly exeeed 45° C and tidal amplitude in the swamp during spring tides often exceeds 1 m. Beginning in March 1987, we placed nest boxes made of salt-treated pine or red cedar at 100 m intervals along the ereek banks. Box dimensions were 28 L × 9 W × 6 D em and the entrance hole was 3.8 cm in diameter (see Blem and Blem 1991, 1992, 1994, for details). We gradually increased the number of nest boxes in the study from 141 in 1987 to 300 in 1993–1998.

We ehecked the eontents of boxes 8–15 times during each breeding season. Old nest material was removed from the boxes in late winter. Eggs that failed to hateh were opened to determine fertility and degree of development. The present paper ineludes only those elutehes that were ineubated by females and only those eggs that failed to hateh because of infertility. Clutches that failed because nests were abandoned were not ineluded in the analyses. Parasitism by Brown-headed Cowbirds (*Molothrus ater*) is relatively uneommon at our study site (<5% of all elutehes), but nests eontaining eowbird eggs were excluded from our analyses. We recorded dates of first eggs and clutch sizes only for those nests visited often enough that we could be eertain of laying dates. In some instances, we determined clutch size but nests were subsequently taken by predators and we were unable to determine fertility of the eggs. Sample sizes therefore vary among various subsets of the data. Because Prothonotary Warblers typically produce two clutehes each season (Petit 1989, Blem and Blem 1992), we divided nests with eggs into two groups: first elutches in which first eggs were laid from 25 April through 20 May and second clutehes in which first eggs were laid after 20 May. Reeaptures of banded birds indieated that this division was aeeurate for this data set. Nest boxes were originally attached to trees. We moved them to metal poles in 1995, almost eompletely eliminating predation on nests. Since then many females have been reeaptured during seeond broods in the same nest box. We eaptured adults by hand-netting them as they emerged from boxes and banded all birds with aluminum USFWS bands. In 1998, we used the eriteria in Pyle (1997) to age adults, but older adults and many birds eaptured before 1998 could only be aged relative to previous eaptures. We designated sueh birds with a + (i.e., 3+) to indicate minimal age, and analyzed age elasses accordingly.

All data are reported as means ± SD. Differenees among groups were analyzed using nonparametrie Kruskal-Wallis tests (χ^2 approximation; Zar 1984, SAS Institute Ine. 1990, Proe NPAR1WAY). In all statistical tests, a probability of 0.05 or less was accepted as signifieant ($P < 0.05$). All analyses were performed using SAS (Ver. 6; SAS Institute, Inc. 1990) on an IBM mainframe computer (VM operating system).

RESULTS

Sample size.—Over the 12 years we banded 2968 nestlings and 482 adult females. Birds were recaptured opportunistically, therefore sample sizes varied from year to year and individual age classes came from various years. We recovered 487 adults and 103 birds banded as nestlings. Recaptures during the same clutch were counted only once. Of all females banded as adults, 47.9% were recaptured at least once in subsequent years ($n = 231$). Only 1.7% of all nestlings were recaptured ($n = 50$). Some females ($n = 112$) were captured over several years and, therefore, are represented in several age classes in Tables 1 and 2.

Clutch size.—We obtained 1033 clutch sizes from 281 female Prothonotary Warblers of known age (Table 1). First clutch sizes differed significantly among age classes ($\chi^2 = 22.4$, $P = 0.002$, df = 7), but there was no difference in second clutches ($\chi^2 = 5.0$, $P > 0.05$, df = 7). One year old female Prothonotary Warblers laid an average of 0.4 fewer eggs in first clutches (4.64 ± 0.48; $n = 42$) than did older females (5.03 ± 0.73; $\chi^2 = 17.7$, $P < 0.001$, df = 1; Table 1). First clutches did not differ among age classes of birds older than one year ($\chi^2 = 4.6$, $P > 0.05$, df = 6). First clutches of all birds averaged 1.01 eggs more than second clutches (4.96 ± 0.72 vs 3.94 ± 0.55; $\chi^2 = 356.8$, $P < 0.001$, df =

TABLE 1. Clutch size of known-age female Prothonotary Warblers captured at Presquile National Wildlife Refuge, Virginia.

Age (years)[a]	First clutches[b]	Second clutches[b]	Julian date of first egg[b]
1	4.64 ± 0.48 (42)	3.81 ± 0.60 (11)	125.0 ± 6.4 (40)
1+	4.91 ± 0.72 (395)	3.86 ± 0.62 (128)	124.1 ± 5.5 (381)
2	4.94 ± 0.79 (33)	3.90 ± 0.32 (10)	123.2 ± 5.6 (32)
2+	5.04 ± 0.79 (211)	4.06 ± 0.46 (65)	121.4 ± 5.8 (205)
3	5.20 ± 0.42 (10)	4.25 ± 0.50 (4)	120.3 ± 2.5 (10)
3+	4.97 ± 0.59 (58)	4.12 ± 0.33 (17)	121.3 ± 6.2 (55)
4	4.50 ± 0.71 (2)	— (0)	121.0 ± 4.2 (2)
5–8	5.18 ± 0.53 (33)	4.00 ± 0.39 (14)	121.0 ± 6.1 (32)
Totals	4.96 ± 0.72 (784)	3.94 ± 0.55 (249)	123.0 ± 5.8 (757)

[a] Plus signs indicate that females were that age or older.
[b] Numbers in parentheses are sample sizes. Values are means ± SD.

1; Table 1). The mean of second clutches of one year old birds was 0.24 eggs fewer than that of females 2–8 years old (3.81 ± 0.60 vs 4.05 ± 0.54), but did not differ significantly among the age classes ($\chi^2 = 9.1$, $P > 0.05$, df = 5; Table 1). We found no change in clutch size over consecutive years for 82 of 122 individuals; in 24 cases clutch size increased by one egg, in 14 cases clutch size decreased by one egg, and in two cases clutch size decreased by two eggs.

Nest initiation dates.—Nest initiation dates (Julian) differed significantly among age classes in the whole data set ($\chi^2 = 54.7$, $P < 0.001$, df = 7), but not among age classes of females 2 years old or older ($\chi^2 = 6.2$, $P > 0.05$, df = 5). One year old birds initiated laying of first clutches significantly later than older birds (125.0 ± 6.4 vs 121.5 ± 5.8; ($\chi^2 = 13.9$, $P < 0.001$, df = 1). The mean date of nest initiation was remarkably stable among females greater than two years old, varying very little from 1 May (Julian date = 121).

Infertility rate.—The number of infertile eggs in first clutches was significantly larger in one year old females than in older birds ($\chi^2 = 3.9$, $P < 0.05$, df = 1; Table 2), but the number of infertile eggs in second clutches did not differ significantly with female age ($\chi^2 = 8.7$, $P > 0.05$, df = 7). Infertile eggs were more frequent in first clutches than in second ($\chi^2 = 8.8$, $P < 0.01$, df = 1). We found no effect of age on frequency of clutches in which all eggs hatched, regardless of clutch size ($\chi^2 = 0.04$, $P > 0.05$, df = 1). One year old birds hatched all eggs in 36.0% (18/50) of their clutches. Older birds hatched all eggs in 35.6% (235/660) of their clutches and there was no significant difference between the two groups ($\chi^2 = 0.005$, $P > 0.05$, df = 1).

TABLE 2. Number of infertile eggs and nestlings per clutch of known-age Prothonotary Warblers captured 1987–1998 at Presquile National Wildlife Refuge, Virginia.

	Number of infertile eggs		Number of nestlings	
Age (years)[a]	First clutches[b]	Second clutches[b]	First clutches[b]	Second clutches[b]
1	1.00 ± 0.90 (28)	0.43 ± 0.53 (7)	3.70 ± 0.89 (28)	3.43 ± 0.79 (7)
1+	0.55 ± 0.75 (295)	0.42 ± 0.61 (67)	4.41 ± 0.92 (295)	3.58 ± 0.69 (67)
2	0.92 ± 1.41 (26)	0.50 ± 0.68 (10)	4.04 ± 1.64 (26)	3.40 ± 0.71 (10)
2+	0.66 ± 0.88 (179)	0.47 ± 0.79 (49)	4.36 ± 0.94 (179)	3.61 ± 0.86 (49)
3	0.90 ± 1.20 (10)	0.50 ± 0.71 (2)	4.30 ± 1.25 (10)	3.50 ± 0.71 (2)
3+	0.71 ± 1.01 (45)	0.21 ± 0.43 (14)	4.31 ± 1.18 (45)	3.86 ± 0.36 (14)
4	0.50 ± 0.71 (2)	— (0)	4.00 ± 0.00 (2)	— (0)
5–8	0.73 ± 0.87 (26)	0.33 ± 0.71 (9)	4.46 ± 1.17 (26)	3.55 ± 1.01 (9)
Totals	0.64 ± 0.87 (611)	0.42 ± 0.69 (158)	4.34 ± 1.01 (611)	3.59 ± 0.77 (158)

[a] Plus signs indicate that females were that age or older.
[b] Numbers in parentheses are sample sizes. Values are means ± SD.

DISCUSSION

In eastern Virginia, Prothonotary Warblers lay 2–8 eggs per clutch and clutch size varies significantly among years (Blem and Blem 1992). In 1986, we initiated a study to identify those factors that were responsible for those yearly differences. To lend explanatory strength to our analyses, we attempted to identify potential sources of variation. For example, date of clutch initiation is significantly related to clutch size (Blem and Blem 1992), while nest cavity volume, position of the nest, presence of old nest materials, and female mass are not (Blem and Blem 1991; Blem et al. 1999, unpubl. data). Female age is related significantly to Prothonotary Warbler clutch size in a manner similar to that found in several other cavity-nesting species (Klomp 1970, Sæther 1990), particularly the European Starling (*Sturnus vulgaris*; Kluijver 1935), House Martin (*Delichon urbica*; Bryant 1988), Pied Flycatcher (*Ficedula hypoleuca*; Sternberg 1989) and Great Tit (*Parus major*; McCleery and Perrins 1989). In all of these species, older females laid 0.4–1.0 more eggs per clutch than birds producing their first clutch. The increase in mean size of first clutches with age may be due to several factors including proximate factors such as increased development of reproductive tracts or enhanced ability to collect and process energy, thus allowing females to produce more eggs.

The effects of senility on clutch size are less well known. There seems to be no documented decreases of clutch size accompanying longevity in passerine birds. This might be due to the difficulty in obtaining clutch sizes from the rare individuals that reach more than a few years of age. In the present study we obtained clutch measurements from several birds more than four years old, including one each from six, seven, and eight year old birds. One female originally caught as an adult in 1990 was recaptured a total of 8 times from 1990–1997. Her first clutch sizes were 4 (1990), 5 (1992), 5 (1993), 5 (1995), 5 (1996), and 5 (1997). In 1997 the bird was at least eight years of age. The previous longevity record for Prothonotary Warblers was 5 years, 11 months (Kennard 1975).

Conservation measures, including intensive use of predator-proof nest boxes, have been successful in increasing local abundance of Prothonotary Warblers (Blem and Blem 1992). However, elimination of predation at nest boxes could skew age structures of warbler populations either by increasing production of young or by decreasing mortality of adult females nesting in boxes. Skewed age structures could then affect clutch size and infertility rates, this factor must be taken into account in any analysis of annual variations in clutch size. For conservation of the species, reduced clutch size and greater infertility of young birds seem to have only a modest impact on reproductive performance of Prothonotary Warblers. Furthermore, effects of senility were not obvious even in relatively old warblers.

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Hybridization Between Clay-colored Sparrow and Field Sparrow in Northern Vermont

David J. Hoag[1]

ABSTRACT.—A male sparrow showing hybrid characteristics between Clay-colored (*Spizella pallida*) and Field sparrows (*Spizella pusilla*) was first observed in Grand Isle, Vermont, in 1997. In 1998, the same hybrid defended a territory and mated with a female Field Sparrow. The pair produced one fledgling. The hybrid's signature song was composed of the buzzy notes of a Clay-colored Sparrow rising to a final trill as if copying a Field Sparrow's accelerating clear whistles. *Received 18 Dec. 1998, accepted 9 May 1999.*

I have found only two previous records of Clay-colored Sparrows (*Spizella pallida*) and Field Sparrows (*Spizella pusilla*) cooperating at a nest. Finch and Smart (1974) mention, without further details, a Clay-colored Sparrow found breeding with a Field Sparrow at Rockefeller Institute, Dutchess County, New York; "young were taken for study." The one example of hybridization presented by Knapton (1994) is the account by Brooks (1980) of a trio of adults, a male Clay-colored Sparrow and a pair of Field Sparrows, at a nest near Millbrook, Dutchess County, New York; however, "the fledged young appeared identical to young Field Sparrows." Carey and coworkers (1994) refer to the same report as "possible" hybridization. Hybridization between these two species is not unexpected because of their close phylogenetic relationship (Patten and Fugate 1998). Examples exist of apparent crossbreeding between Clay-colored Sparrows and other *Spizella* species, and between Chipping Sparrow (*Spizella passerina*) and Brewer's Sparrow (*Spizella breweri*; Knapton 1994, Pyle and Howell 1996).

Clay-colored Sparrows are rarely reported in Vermont (Faccio et al. 1997, 1998). In contrast, Field Sparrows may be abundant in proper habitat such as the abandoned overgrown fields and pastures of Grand Isle, a town on Lake Champlain in northwestern Vermont. There, on 29 May 1997, I identified a Clay-colored Sparrow by its song which consisted of two long buzzes. At 09:30, 11:00, and 16:30 EST, for a total of 30 minutes, I listened to the sparrow sing from elevated perches in a grassy clearing surrounded by red cedar (*Juniperus virginiana*), staghorn sumac (*Rhus typhina*), and common barberry (*Berberis vulgaris*). This sparrow was relocated 650 m north on 2 June, and last heard on 5 June.

From 23 July through 14 August, I observed and recorded a second Clay-colored Sparrow in a similar clearing 300 m southwest of the original location. I recorded the songs on a microcassette recorder and transferred the songs to a computer using either Creative

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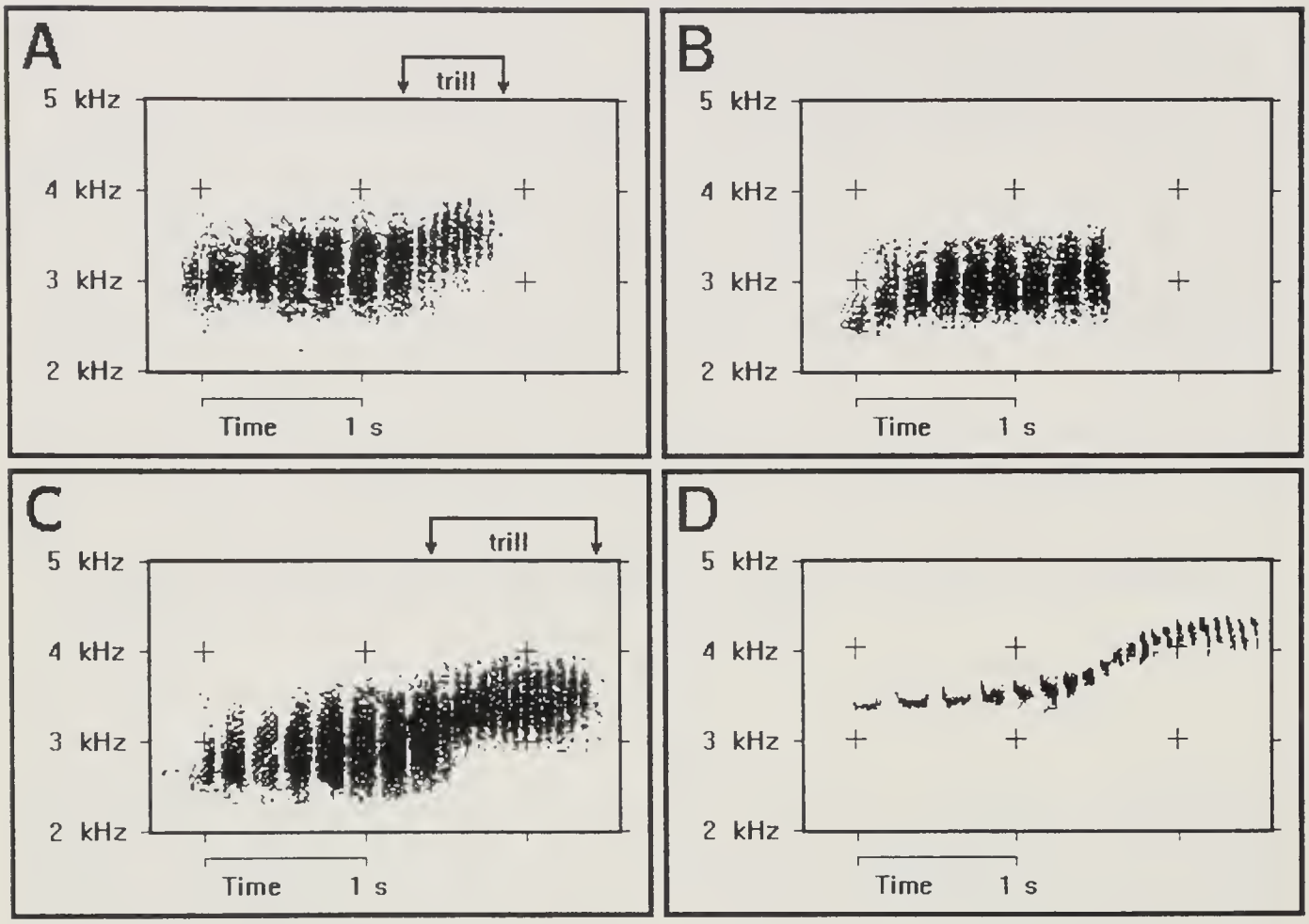

FIG. 1. Three sonograms illustrate the buzzy songs of the probable Clay-colored/Field Sparrow hybrid. A. Trilled version of the hybrid Clay-colored Sparrow's song recorded July 1997. B. Basic song of the same hybrid Clay-colored Sparrow recorded May 1998. C. Trilled version of the same hybrid sparrow's song recorded May 1998. The two trilled songs have a very similar pattern to a Field Sparrow's clear whistles as illustrated by D. D. A Field Sparrow's basic song recorded May 1998.

Technology's Sound Blaster Pro Voice Editor version 2.08, or Microsoft Windows Sound Recorder version 3.1. The sonograms were created in Windows 3.1 with Spectrogram (version 2.3; Horne 1995).

I assumed this second bird was a different Clay-colored Sparrow because its song, 5–8 short buzzes, was extraordinarily different from the first bird's song of two long buzzes. The second sparrow's song frequently ended with a buzzy trill that varied in duration (Fig. 1A). With the added trill, the song resembled a Field Sparrow's basic song (Fig. 1D). The sonograms show the similarity of the song pattern to a Field Sparrow song, and show the dissimilarity of the buzzy notes to the clear whistles of a Field Sparrow. The mimicry either was learned from Field Sparrows in the surrounding area (Knapton 1994) or perhaps was a product of hybridization.

Although the face markings of the second sparrow seemed somewhat indistinct, the plumage pattern was generally compatible with Clay-colored Sparrow. The wide central stripe and the streaking on the crown were typical of Clay-colored Sparrow. The shapes of the bill and the tail were also representative of Clay-colored Sparrow. However, the reddish tint of its plumage and the pink color of its entire bill caused me and other observers to accept it as a probable hybrid between a Clay-colored Sparrow and a Field Sparrow. Two observers thought the flank color at the bend of the wing was indicative of Field Sparrow parentage. The Vermont Bird Records Committee agreed with the hybrid designation at its November 1998 meeting (Nicholson, pers. comm.).

From 7–14 April 1998, Field Sparrows returned to the area. On 28 April, on the same territory that had been occupied by the hybrid in July and August of 1997, I found a bird

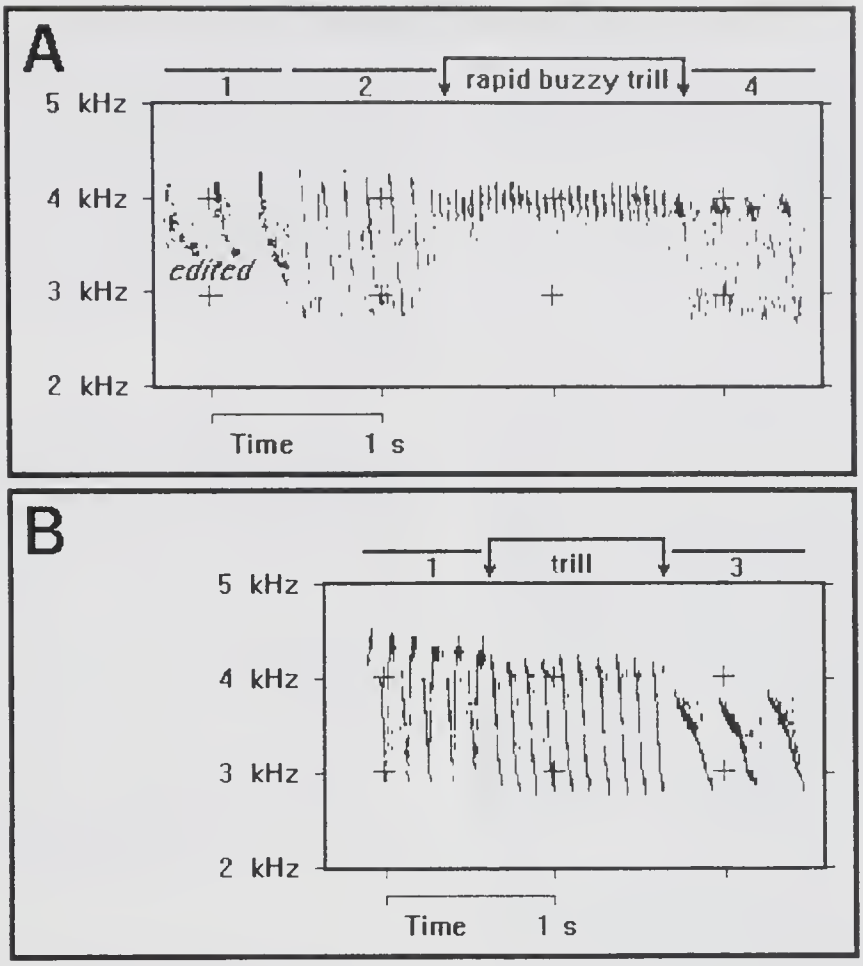

FIG. 2. A Clay-colored Sparrow's mimicry of a Field Sparrow's complex song as illustrated by two sonograms. A. The new Clay-colored Sparrow's four-part song recorded 8 July 1998. B. A Field Sparrow's three-part complex song recorded July 1998.

whose coloration matched that of the hybrid I had seen in 1997. Also, the bird's song was the same distinct vocalization of about eight buzzes (Fig. 1B) with trilled notes occasionally added (Fig. 1C), as heard and recorded in 1997 (Fig. 1A). According to Knapton (1994), Clay-colored Sparrows retain their song type from one year to the next.

On 23–24 July 1997, the hybrid sang rapid eight buzz songs interspersed with seven buzz songs having the added trill. The length of the trill varied; twice it was very short with only three notes. The repertoire from 25 July to 3 August consisted of five buzzes heard 14 times, seven buzzes heard 9 times, seven buzzes with a trill heard 17 times, eight buzzes heard over 50 times, and nine buzzes heard twice. Errors in judging sounds may have affected the true syllable count. The sonograms verify the softness of the initial buzz. In two variant seven buzz songs, the fifth syllable was abbreviated. One long song of faster buzzing was heard on 7 August. In 1998, the hybrid's songs were less variable. I heard few five buzz songs, and seven buzz songs without a trill were very scarce. Approximately 25% of the songs were seven buzzes with a trill; 75% were eight buzzes.

By 3 May 1998, the hybrid had moved about 100 m north. Singing occurred less frequently during the second half of May when the hybrid acquired a Field Sparrow as a mate. I made frequent observations throughout May and June and found no extra Field Sparrows within the territory. I did not observe any extra-pair copulations.

Nest inspections at 09:00–10:30 revealed no egg on 4 June, one egg on 5 June, two eggs on 7 June, and three eggs on 8 June, the first day that the Field Sparrow was brooding. On 19–23 June, the female sparrow sat on the nest, blocking viewing of the nest contents. Both adult sparrows carried food to the nest 21–26 June. On 28 June, the abandoned nest contained two infertile eggs. Both adults chaperoned me and chipped continuously as I at-

tempted to view the single fledgling at 07:45 and 13:35. The hybrid carried food on 2 and 5 July and continued to scold me throughout July. On 26 July, the hybrid guarded the juvenile. The two adults and the juvenile were still in close association.

The female Field Sparrow's reaction during my unsuccessful search for a second nest on 26 July indicated that a second brood existed. I saw the hybrid carrying food again on 5 August, a late date for assisting the first brood juvenile hatched approximately 40 days earlier. In December 1998 I found the second nest which was obscured by grass within a thicket of barberry centrally located in the 0.3 ha territory. This second nest contained one Field Sparrow egg. Since all 1997 Field Sparrow nests in the surrounding area were destroyed by ice accumulation during three days of freezing rain in January 1998, this undamaged nest provided additional evidence that the hybrid and its mate raised a second 1998 brood.

I did not hear the hybird singing from mid-June until 5 July, the day a new Clay-colored Sparrow began a four day encroachment upon the territory. The new Clay-colored Sparrow's song (Fig. 2A) closely resembled a Field Sparrow song (Fig. 2B). All songs of this new Clay-colored Sparrow were identical except for minor variations in length. The hybrid responded with its own songs (Fig. 1A–C) through 12 July.

The ability of some emberizid sparrows to learn other species' songs (Tasker 1955, Baptista et al. 1981), possibly useful in defense of territory, may also attract mates from closely related species. Albrecht and Oring (1995) indicated that the primary function of song for Chipping Sparrows is mate attraction rather than territorial defense. The song mimesis may result in occasional interspecific pairing of *Spizella* species. Unpublished accounts of *Spizella* mimesis include Chipping Sparrows and Clay-colored Sparrows singing each other's song (Bailey, pers. comm.) and a Field Sparrow singing a Chipping Sparrow song (unpubl. data).

The probable hybrid's unusual plumage, its atypical song, its pairing with a female Field Sparrow, and its intensive parental activity at the nest imply that crossbreeding between Clay-colored Sparrows and Field Sparrows occurs. A DNA study of these individuals might verify hybridization.

Note added in proof: The hybrid sparrow returned 5 May 1999 and eventually paired with a female Field Sparrow 9 July to 2 August. His songs in 1999 initially were identical to those in 1997 and 1998, but stopped including the trill during the last half of the breeding season.

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Commentary

A CRITIQUE OF WANG YONG AND FINCH'S FIELD-IDENTIFICATIONS OF WILLOW FLYCATCHER SUBSPECIES IN NEW MEXICO

John P. Hubbard[1]

In a recent paper in the *Wilson Bulletin*, Wang Yong and Finch (1997; henceforth Y&F) reported that they subspecifically identified 83 of 84 Willow Flycatchers (*Empidonax traillii*) captured, banded, and released in central New Mexico in spring and autumn 1994 and 1995. Given the nature of these subspecies and the means by which Y&F apparently identified them, I am extremely doubtful about the reliability of their determinations and thus the validity of these as scientific data. The fact is that identifying these taxa is quite difficult, even for trained taxonomists working in the laboratory under the best protocols and conditions. This difficulty stems from a number of factors, the major one being the pervasive subtlety of the plumage-color characters by which these subspecies mainly differ. Not surprisingly, these differences are difficult to describe in words, which is exacerbated by the fact that none of the available classification systems accurately portrays the range of plumage coloration observed in this flycatcher (e.g., Browning 1993). This means that this species' plumage-color characters are best observed in specimens (i.e., study or flat skins), which also provide the best avenue for identifying subspecies. To do this, one must first assemble series of skins representing all relevant taxa, as well as such important subcategories as age classes (e.g., adult vs immature) and seasonal groupings (e.g., spring vs autumn). Then one sorts "unknowns" (which could include live birds) into subcategories and compares them to the taxa therein, which should produce at least tentative subspecific identifications. In fact, this is the standard laboratory approach for identifying color-based subspecies, and it is the only means proven reliable for this purpose in the Willow Flycatcher.

As my earlier comments suggest, I do not believe Y&F used the approach described above in their attempts to identify subspecies in the Willow Flycatcher. In other words, they did not take synoptic series of study skins into the field, against which the birds they captured were compared to determine subspecific identities. However, I cannot be 100% certain about this because the methods section in their paper is so incomplete and otherwise deficient one can only guess at many aspects of their approach. Nonetheless, it seems logical that if they had used skins as the basis for their identifications, they would have said so. Given this assumption, if they did not use skins, how did they go about identifying their birds to subspecies? On this matter Y&F are at best vague, providing a few clues but no definitive explanations of their identification methodology. For example, we are told that they ". . . adopted the four-subspecies classification system of Hubbard (1987) and Unitt (1987)," in which "subspecies identity . . . is based [in part] on . . . coloration of the head [= crown] and neck [= forenape] and its contrast with the back, and the contrast between the breastband and the throat (see Phillips 1948, Hubbard 1987, Unitt 1987, Browning 1993)." Based on this, I assume that Y&F chose literature descriptions (as opposed to specimen comparisons) as the basis for their identification of Willow Flycatcher subspecies. In addition, I also suspect they converted these descriptions into the color values of Smithe (1975), as this is the system they used to classify coloration in birds captured in the field. Beyond this, one could also speculate on such matters as (a) how converted values were actually used to identify birds, e.g., whether in a dichotomous key, probability table, or other

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framework; or (b) what Y&F's perceptions were of color characters in various races, given that no such descriptions were offered by them. However, I see no purpose in further speculation concerning these or other aspects of their methodology. This is because if they did base their identifications on the literature rather than specimens, I believe the process became so flawed that the details are irrelevant—like rearranging deck chairs on the sinking Titantic!

The message here is that the literature is no substitute for specimen comparisons for anyone attempting to identify Willow Flycatcher subspecies, at least if attaining the most reliable scientific data is the goal. Furthermore, given logistical and other problems, I doubt even specimen comparisons would consistently yield reliable identifications of live birds under field conditions. Not only would it be unwieldy to take and use museum skins in the field, but setting up and maintaining constant conditions (e.g., lighting) would also be difficult. In addition, except for recaptures, only one opportunity would be available to identify each live bird in the field. This means that one could not reassess identifications at a later time, which is both frequent and necessary when studying specimens in the laboratory. In this regard, photographs and certainly color readings (e.g., from Smithe 1975) would not be adequate for such reexaminations because these do not exactly duplicate colors observed in the birds or specimens themselves. Given these considerations, I believe that identifying subspecies in the Willow Flycatcher is best done in the laboratory, using study skins examined under proper protocols and procedures by people trained in the process. In other words, this is a task that should be left to an alpha-taxonomic approach, which is appropriate when one considers that subspecies arose and largely remain as products of that realm.

Even when approached as outlined above, the reality is that not every specimen or even population of this flycatcher can be reliably assigned to subspecies. Intergradation and overlap occur in all characters that distinguish these taxa, so birds exhibiting such characteristics may be un- or misidentified as a result. In addition, characteristics in some populations remain poorly known, mainly because of the paucity of specimens from these areas. For example, in the latest revision of the species, Browning (1993) could only assemble 270 specimens of breeding season adults—including fewer than 20 of the endangered subspecies *E. t. extimus* of the Southwest. As a consequence, it is not surprising that he questioned boundaries between four of the five subspecies recognized in his paper. Even when populational characteristics are better known, opinions may differ as regards their taxonomic treatment. Thus, Browning (1993) recognized two subspecies (i.e., *E. t. traillii* and *E. t. campestris*) as breeding in the region east of the Rocky Mountains, whereas Unitt (1987) merged the latter with the nominate form. Differences in opinion also exist on a broader scale, such as concerning the overall number of subspecies recognizable in the Willow Flycatcher. For example, some taxonomists maintain that none should be recognized (e.g., Mayr and Short 1970, Traylor 1979), while others accept four to six as valid (e.g., Phillips 1948, Aldrich 1951, Wetmore 1972, Oberholser 1974, Unitt 1987, Browning 1993). Thus, although specimen comparisons provide our only reliable means for identifying subspecies in this flycatcher, this approach must be used with the clear recognition that it is just the first step in this very difficult endeavor.

Incidentally, the above differences in taxonomic opinion present a problem for those that rely largely or entirely on the literature for their knowledge of geographic variation in this species. That is, how does one choose which authorities to follow and thus which viewpoints to accept on this subject? Among others, one way around this would be to adhere strictly to a single point of view, such as the recent revision of this flycatcher by Browning (1993). However, Y&F chose not do this, instead electing to cobble their concept of variation from a variety of sources (e.g., Phillips 1948, Hubbard 1987, Unitt 1987, Browning 1993). Given the lack of consensus among these sources, this was a questionable decision. In fact, it would be a challenge even for people with firsthand experience with geographic variation in this species, as seen from the variety of opinions cited above. As a consequence, it is not surprising that I would quibble with Y&F's choices, including that of which authorities to follow.

For example, as indicated earlier, they cited my unpublished paper (Hubbard 1987) as a basis for the "four-subspecies classification system" adopted in their study. However, that so-called system was actually a cobbling job itself, my aim being to summarize color characters of various subspecies from the treatments of Phillips (1948), Aldrich (1951), Wetmore (1972), and Oberholser (1974). As such, it was not meant either to provide definitive descriptions of these subspecies or to recommend which should be recognized as valid. For it to have been otherwise used by Y&F may seem flattering, but it certainly was not a sound decision from a taxonomic viewpoint.

Given the flawed nature of their approach, it is no surprise that Y&F's findings on Willow Flycatcher subspecies would also be open to question. For example, when compared with what is known from specimens (e.g., Hubbard 1987), significant differences emerge on the New Mexico status of three of the four taxa recognized in that study. (In light of the relative scientific standing of the two sources, I would obviously accept the specimen version over that of Y&F in every case.) The most significant difference occurs in the subspecies *E. t. brewsteri* (sensu stricto), which breeds along the Pacific slope of North America. Although occurring regularly in migration eastward to Arizona (Monson and Phillips 1981), this form has rarely been collected east and north of that state, e.g., in Utah (Behle 1985), Colorado (Bailey and Niedrach 1965), Oklahoma (Sutton 1967), and Texas (Oberholser 1967). Hard data from New Mexico clearly conform to this pattern, with only two (4.7%) of the 43 specimens so attributed in Hubbard (1987) and even these were somewhat equivocal. By contrast, Y&F identified 33 (39.8%) of their 83 birds as *E. t. brewsteri,* which is about 8.5 times more frequent than reported by Hubbard. Another notable departure involves the subspecies *E. t. traillii* (in which Y&F include *E. t. campestris*), which breeds from the Great Plains to the northeastern Atlantic Coast. In the Southwest, *E. t. traillii/campestris* occurs regularly in the plains of eastern Colorado (Bailey and Niedrach 1965) and New Mexico (Hubbard 1987), but it has not been collected as far west as Arizona (Monson and Phillips 1981). Yet Y&F reported that 8.4% of their birds were this form, even though the the middle Rio Grande Valley lies some 200 miles west of the nearest specimen localities in New Mexico. Finally is the race *E. t. adastus,* which breeds widely in the interior U.S. north of the southwestern states, through which it passes in both spring and autumn. In New Mexico, it comprised 25.6% of the specimens reported by Hubbard (1987), compared to 10.8% in Y&F's sample.

As for the fourth subspecies (*E. t. extimus*), Y&F identified 34 (41.1%) of their birds as this form, compared to the 48.8% from throughout New Mexico by Hubbard (1987). Thus, on the face of it, their findings would seem not to differ significantly from what is known from specimens of this taxon. However, the number of questionable literature records of this subspecies suggests it may be more subject to misidentification than certain other forms, such *E. t. brewsteri* and *E. t. traillii* (both sensu lato). Birds that might be mistaken for *E. t. extimus* could include sunbleached or worn individuals of other races, as well as pale variants of *E. t. adastus,* intergrades between the latter and *E. t. extimus,* and carelessly-examined *E. t. campestris.* If so misidentified, such instances could help explain records of *E. t. extimus* from areas outside its known breeding range, such as the northern two-thirds of Colorado (Bailey and Niedrach 1965) and Texas east of the Trans-Pecos region (Oberholser 1974). As for New Mexico, I am dubious of *E. t. extimus* records from the eastern plains, such as two specimens reported in Hubbard (1987) from Roosevelt County. In addition, I have definitely reidentified two of the purported *E. t. extimus* from that report, one from San Juan County (= *E. t. adastus* > *extimus*) and another from Socorro County (= *E. t. extimus* > *adastus*). Of course, as mentioned earlier, we do not have the luxury of reexamining *E. t. extimus* (or other subspecies) reported by Y&F, so their identifications cannot be reassessed in light of potential sources of misidentification. Given this and their flawed methodology, I see no reason to regard their findings on this form as any more acceptable than those on the other races reported in their paper. As a final point, Y&F make no mention of the differences between their findings on the various subspecies and the specimen record as discussed above.

While the need for this would not have been obvious as regards *E. t. extimus* and perhaps even *E. t. adastus,* this could hardly have been the case with *E. t. traillii* and especially *E. t. brewsteri.*

To summarize, geographic variation in the Willow Flycatcher mainly involves subtle differences in plumage coloration, concerning which taxonomists disagree in terms of the number of subspecies that should be recognized. Anyone contemplating identifying these subspecies should do so with these caveats in mind, as well as by approaching the process through the use of specimen comparisons—preferably in the laboratory under controlled conditions and with proper training in alpha-taxonomic procedures. Given that Y&F's approach appears to have been otherwise, I submit that their field identification of these subspecies cannot be regarded as a bona fide assessment of this parameter in the birds they processed in New Mexico in 1994 and 1995. Furthermore, for those that would use their subspecific findings, I urge them to do so with extreme caution to say the least. Beyond this, I would like to state that as an alpha-taxonomist, I am dismayed that a study with such a flawed approach to subspecies identification could make its way into print in a major ornithological journal. To wit, ornithology has come to rely almost entirely on non-specimen data for monitoring the distribution and status of birds on this planet. While not necessarily a bad thing, sometimes we may fail to recognize the very real limitations of such data. No better example of this exists than as regards the identification of difficult taxa, of which subspecies in *Empidonax traillii* provide a perfect case in point.

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RESPONSE

Wang Yong[1] and Deborah M. Finch[1,2]

Hubbard (1999) criticizes our paper *Migration of the Willow Flycatcher along the middle Rio Grande* (Yong and Finch 1997), where we reported aspects of stopover ecology of the species including timing, abundance, fat stores, stopover length, and habitat use. Hubbard questions our identification of subspecies of the Willow Flycatcher (*Empidonax traillii*) and the methods we used to identify them. He also attempts to evaluate the accuracy of our results of subspecies composition by comparing them with data from other researchers. We welcome and applaud this scrutiny in the hope that this interchange will stimulate greater interest, research, and capability to distinguish the phenotypic characteristics of subspecies of the Willow Flycatcher. Given that the southwestern race (*E. t. extimus*) of the Willow Flycatcher is federally listed as Endangered, reliable methods for identifying this subspecies need to be developed to more effectively conserve and recover its populations.

We are aware that the subspecific taxonomy of the Willow Flycatcher is inconsistent among taxonomists as are the techniques to identify subspecies. Consequently, reliable identification of subspecies is difficult, especially in field situations. We acknowledge that issues of taxonomic status, population distributions, and identification methods of subspecies of the Willow Flycatcher should be explored further. However, Hubbard's criticisms of our paper are generally based on erroneous information as well as incorrect assumptions about our methods, and they do not alter our conclusions about Willow Flycatcher stopover ecology at the species level.

Hubbard's first criticism focuses on the methods we used for identifying the subspecies. Rather than using an assemblage of subspecies skins as advocated by Hubbard to identify Willow Flycatcher subspecies in the field, we relied on descriptions and records of coloration and morphology published in the available literature by taxonomists. Contrary to what Hubbard speculates, we did not convert color descriptions into Smithe's (1975) color code values. We based our identification of back plumage color on the most recent research by Unitt (1987) and Browning (1993). Using Smithe's color codes to describe back plumage, Unitt (1987) writes: "In *brewsteri* the green is in the direction of olive green (color 48), in *adastus* in the direction of greenish olive (color 49), and in *extimus* and *traillii* in the direction of grayish olive (color 43). That is, *brewsteri* is a dark brownish olive, *adastus* a dark grayish green, and *extimus* and *traillii* a pale grayish green. . ." Browning (1993) suggested that Smithe's color system is problematical because the color swatches generally are not identical matches for actual colors. Hence, he used Munsell Color Charts (1990) to describe the crown and back contrast for his specimens. During our fieldwork, we consulted both Unitt's (1987) color codes for subspecies' back color and Browning's color contrast scores between crown and back. Although Hubbard suggests that live specimens have some disadvantages, we counter that the plumage coloration of live birds is more likely to be true to type than skin specimen plumage that may have faded. If our hypothesis that the coloration of fresh plumage differs from that of faded plumage is correct, then data collected from live specimens may be more reliable, or at least not less reliable, than results obtained from study skins. Birds occasionally called or sang in our study after being released. Information about song and call characteristics were also recorded when possible. Such data are available from living flycatchers but not from skins. Sedgewick's (pers. comm.) preliminary analyses of Willow Flycatcher song and call signatures collected

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in different regions suggest that *E. t. extimus* song structure can be distinguished from that of its northern conspecifics and we used this kind of data to aid identification also.

We did not rely solely on coloration for subspecies identification, contrary to Hubbard's second assumption. Unitt (1987) suggested that wing formula (relative length of primary feather length) can be used to assist subspecies identification. Of the 305 specimens that Unitt (1987) examined, wing formula distinguished 93% of the *E. t. extimus* and *E. t. traillii,* 88% of the *E. t. adastus* and *E. t. traillii,* and 89% of the *E. t. brewsteri* and *E. t. traillii.* Browning (1993) also applied wing formula to assess variation in subspecific characteristics, and his results also demonstrated that wing formula may be useful for distinguishing some subspecies although his sample size was smaller than Unitt's. Hubbard himself (1987) noted that *E. t. brewsteri* was smaller than other described forms. In the field, we relied partly on non-overlapping extreme wing measurements to assist in the identification of this subspecies. In addition, we measured and recorded more than 30 variables from each individual. Following Unitt (1987), we used wing formula to aid in identifying subspecies.

Thirdly, Hubbard (1999) comments that "even when characteristics of populations are better known, opinions may differ as regards their taxonomic treatment" because of limited sample sizes, interbreeding among populations, and differences in taxonomists' methods, views, and findings. Although we agree that taxonomists have been inconsistent in their treatment of subspecific taxonomy, we consider this to be an incentive for finding areas of common ground among researchers, rather than a justification for concluding that reliable identification of subspecies is impossible. Hubbard states that we should have strictly adhered to a single view of subspecies taxonomy. We followed a single view of subspecies treatment, but we did not credit this single view to a single researcher. We made it clear that we adopted the "four subspecies classification system of Hubbard (1987) and Unitt (1987)." We warned readers in our Methods section that: "Given morphological overlap and hybridization among subspecies, complete accuracy in identifying subspecies is not achievable." Although taxonomists disagree in their interpretations of within-species variation and subspecies recognition, there is unmistakable agreement about use of a four subspecies classification among recent research papers (Hubbard 1987, Unitt 1987, Browning 1993). Hubbard (1987) clearly advocates acceptance of the four subspecies classification in his report by stating that: "Given the degree of agreement among recent workers, I believe the most prudent course is to accept all of the above subspecies [i.e., *E. t. extimus, brewsteri,* and *adastus*] and *traillii* as valid—at least until more definitive studies are available." Although in his commentary Hubbard declares his own report to be a "cobbling job", its quality is deemed sound by other authorities. Indeed, it has been widely distributed and cited both unofficially and officially by the Endangered Species Programs of U.S. Fish and Wildlife Service regions, by state Game and Fish Departments, and by other agencies and ornithologists in the western United States, especially in the Southwest. Given Hubbard's background as a competent taxonomist in New Mexico and as an officer of the state endangered species branch, his paper is judged as an authoritative source on the species. For example, in the process used for listing the southwestern Willow Flycatcher as a federally endangered subspecies, Hubbard's paper was one of the most heavily cited reports by the U.S. Fish and Wildlife Service (1995).

Unitt (1987) also states that the four races of *E. traillii* are valid and may be distinguished from each other by "color, wing formula, or both". Browning (1993) further separated subspecies *E. t. traillii* into two populations: *E. t. campestris* of the Great Plains and Great Lakes regions, and *E. t. traillii* to the southeast of *E. t. campestris.* We recently became aware, that Unitt has conducted further research on the same specimens and may soon be updating his taxonomic treatment (P. Unitt, pers. com. through J. E. Cartron). These different authors describe subspecies distributions that are very similar although population boundaries are not exactly the same. U.S. Fish and Wildlife Service relied partly on these studies to conclude that listing the southwestern Willow Flycatcher as an endangered subspecies was appropriate.

Fourthly, Hubbard evaluates our results by

comparing our subspecies composition data with subspecies data from his own and other reports and sources. While such comparisons may be valid for the purpose of exploring potential sources of variation, the conclusions that Hubbard draws are incorrect because of spatial and temporal differences among studies. Species, subspecies, and population composition of migratory birds captured at specific stopover sites in fall or spring can dramatically differ from what is observed at the same location during the breeding season at the same location or from other locations during migration. For example, the overall species composition we detected indicated that the majority of individuals captured were not local breeders and many did not even breed in New Mexico (Finch and Yong 1999). While we used a standardized, systematic procedure to sample throughout the entire migration seasons of spring and fall, 1994 and 1995, other studies that Hubbard (1999) cites and compares to ours were not conducted during migration seasons and/or did not use standardized procedures. In addition, source studies cited by Hubbard are heterogeneous in relation to study goals, year of study, number of years, geographical location, sampling design, sampling season, and quality of data, leading to uncontrolled and unknown factors that invalidate comparisons with our data set. Our data are restricted to two sites during two years in the middle Rio Grande valley of New Mexico, and thus are only truly comparable to other data from the same vicinity, year, and sampling design. Given that different studies, especially earlier ones, used controversial criteria for classifying and counting their specimens, Hubbard's argument that our results are inaccurate because they are not completely consistent with other studies that, when compared, also yielded dissimilar results is circular. In our manuscript, we did not make such comparisons for at least two reasons: (1) our research focus was on the stopover biology of the species, not on the taxonomic status of the subspecies, and (2) other data sources were not homogeneous or similar enough to draw comparisons.

Our data and conclusions about the flycatcher's stopover ecology are not dependent on the validity or accuracy of its subspecies status or on the methods used to identify subspecies. Because *E. t. extimus* is endangered, U.S. Fish and Wildlife permits for collecting voucher specimens during migration are not issued in the Southwest, eliminating the possibility of having an alpha-taxonomist identify locally caught specimens to subspecies for the purpose of setting standards. Because most current research studies and conservation efforts pertaining to the Willow Flycatcher have focused on its breeding grounds, the importance of our research centers on when, where, and how migration stopover sites in riparian woodlands along the middle Rio Grande are used for resting and fat depositions by the species. Without understanding the migration strategy of the species and without justifying efforts to conserve the stopover habitat that the species uses, the Willow Flycatcher's fate in the Southwest will be jeopardized regardless of how perfect or imperfect our ability in identifying subspecies is.

Throughout ornithological history, subspecies classification and identification have traditionally been a "problematic" area, particularly within the genus *Empidonax*. Uncertainties about subspecies or even species status do not negate the value of our migration research or refute our results about Willow Flycatcher stopover ecology or intraspecific variation in migration patterns. We assert that increased knowledge of the stopover behavior and energetic condition of the Willow Flycatcher is important for understanding the biology of the species as a whole and that information about within-species variation is valuable in conserving the endangered southwestern subspecies.

Our paper and Hubbard's (1999) critique have opened up the opportunity to develop and expand discussion and evaluation of the different subspecies, the subspecies concept as a whole, and whether subspecies should be recognized for the Willow Flycatcher given the disagreement about their identification and the difficulty in identifying birds in hand. We invite and challenge others to contribute ideas and knowledge to this controversy in the hope that new or better techniques for identifying willow flycatcher subspecies may result. Such discussion or results would certify beyond a doubt the worthwhile contribution of our paper. Subjecting any paper to a critical commentary, however, automatically attracts the

notice of additional readers. We are pleased with the extra attention in the hope that further research, understanding, and conservation efforts will be directed toward the endangered southwestern Willow Flycatcher and its disappearing habitat.

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Ornithological Literature

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THE AUKS. By Anthony J. Gaston and Ian Jones, illustrated by Ian Lewington, line drawings by Ian Lewinton and Ian Jones. Oxford University Press, New York, New York. 1998: xx plus 349 pp., 8 color plates with caption figs., 41 figures, 32 maps, 43 tables 29 photographs. ISBN 0-19-8540320-9. $75 (Cloth).—This book summarizes the biology of these northern seabirds. The authors have spent much time studying many species of auks and are well prepared to summarize the biology of these northern seabirds. As the authors point out, these birds are primarily marine organisms but most studies have been conducted at their breeding sites on land.

The book includes three sections: Plan of the book, General chapters, and Species accounts. The Plan of the book is comparable to the introduction in most books: it explains the intent of the authors and the layout of the book. This section includes an important table presenting common nomenclature between Europe and North America. The plates of the species are excellent. Literature coverage is extensive. The book is written in British English rather than American English.

The General chapters include 7 chapters: *Auks and their world, Systematics and evolution, Distribution and biogeography, Auks and ecosystems, Social behavior, Chick development and the transition from land to sea,* and *Populations and conservation.* These chapters include the authors' understanding of the family, comparative analyses, and syntheses. These are worth the price of the book. These chapters are strong in that they deal with auks at sea as well as the breeding on land. Sections in these chapters are usually one to a few pages in length. As summaries, these cover the material adequately but each could be expanded into a more thorough monograph. Our understanding of these birds has developed slowly because these are marine birds breeding in remote areas. These summary chapters include an important historical perspective when dealing with auks and people, scientific discovery of auks and systematics. These sections allow the reader to put the literature into an historical perspective. We are only now increasingly understanding their marine biology, while often information in the literature is based on early articles based on early assumptions.

The authors discuss the biology of these birds at sea and during breeding at land. Some comparisons are among most auks and related species; some comparisons are among select auk species. These comparisons are important in keeping these birds in perspective with other seabirds, and for understanding how they are adapted to their marine environment. The chapter on populations and conservation is very timely. It includes sections on changes in populations, species of concern, as well as fisheries impacts. While this is a good review, it should have included more timely information on immediate issues. The Species accounts are well written. They include sections on Description, Range and status, Habitat, food and feeding behavior, Displays and breeding behaviour, Breeding and life cycle, and Population dynamics. It would have been nice to include a summary of the conservation status.

This is a fine book with a great deal of information. However, confusion may result from inconsistencies among, and in some cases poor organization of, tables, figures, and maps. Caption formats are different between the General chapters and the Species accounts. Timing of activity at colonies is dealt with inconsistently among the species accounts but is summarized in a table in the chapter on Social behaviour under the confusing heading of Activity timing. Furthermore, in the tables that include measurements in the Species accounts, data are summarized according to reference numbers with no indication as to where to find the references, leaving it to the reader to guess where in the text these reference numbers are indicated. Maps in the first seven chapters have a figure number (without mention of Fig.); among the species accounts,

maps do not contain a figure number or a title, leaving it to the reader to assume that these are for the species accounts in which they are included. Finally, among range maps, the summer range coloration is often difficult to distinguish from the background map coloration. These problems will lead to confusion and detract from an otherwise fine and informative book.

The seven summary chapters present the author's family analyses and strongly based understanding of these birds. This information is well worth the book. The species accounts and difficulty in extracting information are disappointing.—MALCOLM C. COULTER.

THE ECOTRAVELLERS' WILDLIFE GUIDE TO COSTA RICA. By Les Beletsky. Academic Press, San Diego, California. 1998: 426 pp., 80 color plates, 19 habitat photos. $27.95.

THE ECOTRAVELLERS' WILDLIFE GUIDE TO BELIZE AND NORTHERN GUATEMALA. By Les Beletsky. Academic Press, San Diego, California, 1998: 488 pp. 104 color plates, 20 habitat photos. $27.95.

THE ECOTRAVELLERS' WILDLIFE GUIDE TO TROPICAL MEXICO. By Les Beletsky, Academic Press, San Diego, California, 1999: 497 pp. 104 color plates, 21 habitat photos. $27.95.—Each of these volumes is part of a series recently released under the sponsorship of the Wildlife Conservation Society and authored by Les Beletsky. As all of the volumes are quite similar they are reviewed together. The books are intended as ecological introductions. There is a brief opening section about ecotourism that is essentially identical in each of the books, as is the structure of each book. There is an ecological overview of the country followed by chapters on how to use the book and on conservation issues. The major parts of each book are chapters on amphibians, reptiles, birds, and mammals, and, in the Belize book, on marine life. Unfortunately terrestrial invertebrates are totally ignored. There is nothing about butterflies or other prominent inverts in either book. It is disappointing to look in the index and see reference to antbirds, anteaters, antshrikes, ant-tanagers, antthrushes, but not to ants!

Birds are featured prominently in these books, the bird chapter being 89 pages long in Costa Rica, 80 pages long in Belize, 83 pages long in Tropical Mexico (with 50 color plates on birds in each book). Much of the text and plates is duplicated among the three volumes. Chapters on taxa discuss natural history, breeding, ecological interactions, lore and notes, and conservation issues. "Profiled" species are illustrated on the plates. Illustrations are large format and are confined to (arguably) the most common species. For most readers of *The Wilson Bulletin* these guides will not be useful in field identification of birds because too many species are omitted. However, these books will help bird watchers and ornithologists to identify amphibians and reptiles, many of which are not illustrated in convenient field-sized books. As with birds, better and more complete guides exist for mammals and fish. It is regretable that Beletsky selected tropical Mexico, much of which duplicates what he includes in his Belize book, rather than western Mexico, where there are major avifaunal as well as other taxonomic distinctions.

Beletsky's text draws heavily from the published literature and does a credible job of presenting sound overviews of the subject matter. The text ranges widely, from summaries of why some birds have evolved to become frugivores to Mayan legends about how hummingbirds became so bright. Much information, though charming in a way, is superfluous to a utilitarian field guide. The lore and notes sections abound with such quaint insights as the belief that cows belonging to a farmer who has destroyed a swallow's nest will give bloody milk. We are told (in each volume) that the Common Raven (*Corvus corax*) is the largest passerine, though the author readily acknowledges that they do not occur in Costa Rica, Belize, northern Guatemala, or the Mexican Yucatan. I always thought the Superb Lyrebird (*Menura novaehollandiae*) was actually the largest passerine (neither does it occur in the Neotropics).

Nonetheless, visitors to the countries profiled should find the appropriate book useful in gaining a better understanding (and a fair dose of trivia) about the local vertebrate wildlife.—JOHN KRICHER.

A BIRD-FINDING GUIDE TO MEXICO. By Steve N. G. Howell, illus. by Sophie Webb. Cornell University Press, Ithaca, New York. 1999: 365 pp., 54 locality maps. $20 softcover.—This is an exciting addition to the libraries of couch-birders and those eager to bird or investigate new corners of Mexico. This compact and well-organized guide is 6″ × 9″ and appears to be solidly bound. Steve, Sophie, and their occasional fellow travelers have spent hundreds of days and nights in fine resorts, dives, and camping sites to gather locality lists for 111 sites from Baja to the Yucatan. Every locality map is extremely useful to any visitor, although indicated habitat may be altered in time.

This is the first detailed information on many important sites in Mexico, many of which scream for recognition and protection. Very few sites are protected in Mexico. Locality descriptions are well written, to the point, and include attention to directions within a tenth of a kilometer. Comments on availability of second-class buses and camping sites are included for those without their own (or rental) vehicles and those on limited budgets. The species lists are English common names only, and wisely run in 4 columns per page (very economical). Relative abundances are not given, except for those rarely seen. Mexican endemics are bolded in the text and lists.

A variety of taxonomic decisions and English name selections differ from Seventh Edition of the A.O.U. Check-List of North American Birds (1998). Most involve "splits" as both the world bird species list and the Dow Jones Average struggle to pass 10,000. Well-differentiated subspecies clusters are given distinct English names in anticipation of these forms being given full species status in the future. Numbers gathering bird listers pressure for all splits, boo all lumps. One would hope to see less attention by birders focused on one unit of taxonomy and more attention to higher (genus) and lower (subspecies) levels in the future. As for the names selected, it's great to see the use of whitestart replacing redstart for members of the genus *Myioborus*. Redstart was created for Old World thrushes with red on the tail, and is erroneously used for an American parulid which could easily be renamed Orangestart, *Setophaga ruticilla*. There is no red in the tail of any *Myioborus*, most have no red anywhere, and they are no longer placed adjacent to *Setophaga*! Guy Tudor and I came up with whitestart back in the late 1970s as a solution. This British author has sold his publisher on using grey in place of the American gray throughout in contradiction of the 1998 A.O.U. Check-List. I am concerned with using subspecific modifiers in front of species names; it can create much confusion. Perhaps it should be Sooty race of Fox Sparrow or Fox Sparrow (Sooty race) for *Passerella iliaca unaleschensis*, not Sooty Fox Sparrow.

This book is not designed for "lite birders" doing cruises of the Mexican Riviera, the whale lagoons, or the islands of the Gulf of California, nor for those doing single destination beach resort vacations. It will greatly aid self sufficient, street-smart birders and ornithologists with a taste for adventure and great birding. Great job Steve!—PETER ALDEN.

THE BIRDS OF SONORA. By Stephen M. Russell and Gale Monson, illus. By Ray Harm. The University of Arizona Press, Tucson, Arizona. 1998: 360 pp., 2 color plates, 34 b+w figures. ISBN 0-8165-1635-9. $75 hardcover.—A long awaited book authored by two excellent fieldmen who have lived just across the border in or near Tucson for years. This is a fairly heavy book (8½″ × 11″) focused on the ranges, habitats, seasonal abundances, historical records, and current status of over 500 species of birds. It accomplishes its tasks well, especially with the well-researched range maps for most species. This work is the first update in many decades for a province that should attract many more birders from the southwestern states. Sonora has tropical deciduous forest around the colonial hilltown of

Alamos, great pine-oak woodland in the Sierra Madre Occidental, and cactus-scapes of the Sonoran Desert.

The dust jacket features a colorful White-fronted Parrot (*Amazona albifrons*), which is not reproduced within and lost to users of libraries that routinely toss dust jackets. Nice to see the separate large maps of mountain ranges, cities, rivers and reservoirs, and the full color vegetation map in the introduction. I question the wisdom of using only the metric system to indicate elevations and distances. Outside of scientific circles the metric system is dying in the U.S., why obfuscate the majority of the book's users? Add American equivalents in parentheses.

The geographical coverage excludes the Sonoran Islands in the Gulf of California. Isla Tiburon and other islets have no endemic birds and this book should have included a summary of known residents and visitors. While habitat loss is discussed and lamented, a rundown of any protected areas and a focus on areas most in need of protection would have been welcome.

The appendices cover plants named in the text, an exhaustive gazetteer useful to any biologist, and literature cited. Adding a Spanish common name throughout the text and including them in the index is an outstanding step. One hopes this will be made available in Spanish for Sonoran citizens.

Wouldn't it be nice to have similar books state by state throughout Mexico being researched and published in an orderly fashion? This would be a good model.—PETER ALDEN.

A FIELD GUIDE TO THE BIRDS OF MEXICO AND ADJACENT AREAS (BELIZE, GUATEMALA, AND EL SALVADOR), third edition. By Ernest Preston Edwards, principal illustrator Edward Murrell Butler. University of Texas Press, Austin, Texas. 1998: 284 pp. incl 51 color plates. $35 hardcover, $17.95 softcover.—Ernest Edwards has been a pioneer in producing a series of bird-finding guides and compact bird field guides to Mexico. This third edition updates names and taxonomy, adds a few plates, and competes with the Peterson's and Chalif's Field Guide to Mexican Birds (Houghton Mifflin, Boston, 1973). As a portable pocket guide it is significantly wider than the Peterson's (fitting fewer pockets), the artwork a bit stiff and stylized. The text is concise and the book well indexed between text and plates and back. The sequence of families and species in the color plates is jumbled and confusing. Neither book has range maps. Gray is spelled gray not grey in Edwards.

At four times the size and weight of the Edwards or Peterson/Chalif, Steve Howell's and Sophie Webb's *A Guide to the Birds of Mexico and Northern Central America* (New York, Oxford Univ. Press, 1995) is the clear choice for serious students of Mexican birdlife with its exhaustive text, superior plates, and excellent range maps. However, its bulk and weight will force many to consider leaving it at home or in the car when deciding which of the two portable quick reference guides to take in the field. The Edwards book gives much less thought to taxonomic changes and English name modification than does Steve Howell's works, a mixed blessing.

The time has come to stop redoing attempts to cover close to 1100 species of birds from such disparate places in 4–6 countries. What's needed is field guides to Pacific slope birdlife, Gulf and Caribbean slope birdlife, highland birdlife, etc. No matter where you are, one's book has over 50% of its species totally inapplicable to wherever you are. Far more useful would be a guide to, say, just Yucatan, Belize, and Caribbean Guatemala's birds. That's one area that can support such a smaller geographical focus book.—PETER ALDEN.

CHECKLIST OF THE BIRDS OF EURASIA. By Ben F. King. Ibis Publishing, Vista, California. 1997: 105 pp. $19.95 (paper).—Ben King has produced a concise and functional birder's checklist to the contiguous continents of Europe and Asia, plus their attèndant islands, ranging all the way from Iceland to Novaya Zemlya to Japan, the Philippines, the Greater Sundas, and Wallacea, two-thirds of the Old World, in fact. For purposes of distributional coding, King has partitioned this vast expanse into ten regions: Europe, the

Middle East, the former Soviet Union, Japan, the Indian Subcontinent, China, Southeast Asia, the Greater Sundas, the Philippines, and Wallacea. The list follows "generally" that of Peters' world list, and includes 3062 species. Taxonomy is reported to be conservative, although the author notes that he has adopted "some new ideas from the literature as well as unpublished field studies, especially where they appear to corroborate my own experience." The checklist indicates regional presence or absence, but provides no information on status (e.g., breeding, migrant, vagrant) or abundance. The author notes that introduced species are, in many cases omitted. Species endemic to a single one of King's regions are indicated by boldface.

The main focus of King's six page introduction is the construction and clarity of English names. From King's strongly worded statement, it is clear that a main purpose of this checklist was to provide a standardized and revised set of English names for the birds of Eurasia. King notes that names that are elitist or that are difficult to pronounce need to be changed, as do patronyms memorializing westerners. Conducting such a nomenclatural "cleansing" must be a difficult task, indeed. And it is interesting to compare King's bird names against those used in the array of other checklists and field guides for the region. For reasons of space I will focus only on a few widespread Asian passerine species that happen to also inhabit Wallacea, an area familiar to me. For this I refer to the English names used in King and Dickinson's (1975) *Field Guide to the Birds of South-East Asia,* White and Bruce's (1986) *Birds of Wallacea,* Inskipp et al.'s (1996) *Annotated Checklist of the Birds of the Oriental Region,* and Coates and Bishop's (1997) *Guide to the Birds of Wallacea.* At least for these widespread Asian species, the names King today chooses to use are all quite reasonable, and, in fact, the nomenclature across the various publications produced over a 24 year span is surprisingly uniform.

It is rare that one can obtain consensus on English names, even when working in committee. I am happy to report, however, that, at least by comparison of 16 widespread songbird species that served as my sample exhibit vary little variation in name in the six sampled texts. Of these 16, only 4 were represented by more than one name (Red Avadavat/Strawberry Waxbill, Chestnut/Black-headed Munia, Hair-crested/Spangled Drongo, and Eurasian Tree-Sparrow/Tree Sparrow). One of the birds with two names, the drongo, is in fact a geographically variable taxon that may constitute more than a single species. Thus it is evident that even for Southeast Asian birds there is considerable stability and uniformity of English nomenclature. Still, given that King deals with 3000 species, there will be plenty of species with multiple English names in current use. Thus, one of the disappointments of the King checklist is that alternative names are not listed, probably because of space limitations.

The checklist is completed by a comprehensive index of English and scientific names, which lists all scientific names by species (e.g., "*leucophaeus, Dicrurus*") and all English names by group-name (e.g., "Drongo, Ashy"). At the very least I would have preferred to see listing by genus, as well (e.g., "*Dicrurus leucophaeus*"). That complaint aside, this is a compact, well-produced, and useful checklist that covers a huge avifauna. This will be a must buy for many world birders and ornithogeographers.—BRUCE M. BEEHLER.

THE HANDBOOK OF BIRD IDENTIFICATION FOR EUROPE AND THE WESTERN PALEARCTIC. By Mark Beaman and Steve Madge, illus. by Hilary Burn, Martin Elliott, Alan Harris, Peter Hayman, Laurel Tucker, and Dan Zetterström. Princeton University Press, Princeton, New Jersey. 1998: 868 pp., 291 color plates with captions, 77 other color illustrations dropped in the text elsewhere, 625 color-coded range maps, $99.50 (cloth).—This book, originally published in Great Britain by Christopher Helm, is a monumental achievement. It covers almost 900 species known to have occurred in the Western Palearctic, the area defined for the 9-volume Oxford University Press series edited by S. Cramp et al., *The Birds of the Western Palearctic* (1977–1994). This area extends from Franz Joseph Land and Novaya Zemlya south to Kuwait, west to the southwest corner

of Morocco, and north to Iceland, Jan Mayen, and Spitsbergen, including the Azores, Madeira, and Canary Island groups.

All species are illustrated in color, but that is only the beginning. Many are shown in flight, at rest, as adults and juveniles, from above and below, and in several racial forms as appropriate. About 600 of the species covered breed in the area and the rest occur only seasonally or are vagrants. Although a vagrant may have occurred only once or twice, its plumages are covered thoroughly, usually in an illustration dropped in the text, and typically with several images. Vagrants that occur with some frequency are included on the plates with the local species. To provide a perspective on the breadth of coverage, the 33 plates depicting 60 species of jaegers, skuas, gulls, terns, and alcids contain no fewer than 480 images and include at least 12 species that are vagrants from North America or Asia. Two plates and 29 images are devoted to the recently-split Yellow-legged (*Larus cachinnans*), Heuglin's (*L. heuglini*), and Armenian gulls (*L. armenicus*) alone. Swainson's Hawk (*Buteo swainsoni*) has only occurred two or three times, but it rates eight images including both pale and dark morphs, perched and in flight, and even the rare rufous variant. The plates are supported by detailed discussion of identification criteria and comparisons between similar species in the text, including mention of racial populations where current taxonomy is in doubt or where geographical variation is significant.

The same lavish treatment is given every group, including sandpipers and plovers. A high percentage of the shorebird species known for eastern North America is depicted on the plates right next to the most similar Western Palearctic species. Even Eskimo Curlew is there (*Numenius borealis*). Indeed, species such as Semipalmated (*Colidns pusilla*), Least (*C. minytilla*), Western (*C. mouri*), Baird's (*C. bairdä*), White-rumped (*C. fuscicollis*), Stilt (*C. himantopus*) and Pectoral (*C. melanotos*) sandpipers and the two dowitchers are treated more fully than in all but specialized shorebird guides. If anything, Western Palearctic species are even more fully treated. For those with a virtual field-identification death-wish, there are two plates with 32 images of *Phylloscopus* warblers that give new meaning to the notion of confusing (and virtually inseparable) species, including five forms of Chiffchaff (*P. collybita*) that may be made separate species someday.

Though the greatest wealth of detail is reserved, appropriately, for local species, North American birders will be impressed with the description details provided for North American vagrants. Six species of thrushes, 22 wood warblers, 2 tanagers, 15 emberizids, and 5 icterids are covered exhaustively, for example. In addition to critical field marks, variations associated with age or sex, voice, and preferred habitat in each species' natural range are covered in detail, just the same as for local birds.

The taxonomy is relatively conservative and current to about 1995, a significant achievement itself when dealing with so many species. However, the authors have carefully called attention to many races that may be elevated to full species rank in the future: Taiga and Tundra Bean Goose (*Anser fabalis* ssp.), two or more forms of Brant (*Branta bernicla*). Common and Black scoters (*Melanitta nigra* ssp.), Pharaoh Eagle Owl (*Bubo bubo ascalaphus*), two or more Yellow Wagtails (*Motacilla flava*), Moroccan Wagtail (*Motacilla alba subpersonata*), Sykes' Warbler (*Hippolais caligata rama*), the Chiffchaffs mentioned above, and others.

There are brief but excellent introductory sections outlining the content of the species accounts, defining terms, and commenting on the techniques and pitfalls of field identification. Full indices of English and scientific names are provided. There are also appendices of 14 recent additions with full descriptions, another of 50 species intentionally omitted, and an appendix listing other important distribution and identification references for the area covered. As is inevitable in a publication of such size, there are occasional typographical errors, but I noted only three or four in studying the book for over eight hours. Each of the illustrators has done superlative work, and though every plate can be called "good", in this reviewer's opinion there are a few plates that are less successful than others at capturing a vibrant, lifelike quality to the images.

It is easy to lapse into superlatives after only a short acquaintance with this book. It

weighs about five pounds, and at two inches thick it is too large and heavy to fit conveniently in the pocket of a field jacket. But most active North American birders will want to have it, despite the high price, even if they do not always carry it with them. It sets a new high standard for the part of the world it covers, a standard not yet met or even closely approached elsewhere. Highly recommended.—ALLAN R. KEITH.

Wilson Bull., 111(4), 1999, pp. 600–607

PROCEEDINGS OF THE EIGHTIETH ANNUAL MEETING

JOHN A. SMALLWOOD, SECRETARY

The eightieth annual meeting of the Wilson Ornithological Society was held Thursday, 10 June, through Sunday, 13 June, 1999, at Colby College in Waterville, Maine. W. Herbert Wilson chaired the local committee; support for the conference was provided by the Special Programs office of Colby College.

The Council met from 13:07 to 18:27 on Thursday, 10 June, and again from 15:35 to 16:30 on Saturday, 12 June, in Room 335, Olin Hall, Colby College. On Thursday evening there was an informal reception in Cotter Union for conferees and their guests.

The opening session on Friday convened in Room 101 Keys Hall, being called to order at 08:37 by WOS President Edward H. Burtt, Jr. After several announcements were made by Local Chair Herb Wilson and by Scientific Program Chair Ted Davis, President Burtt introduced Professor Ed Yeterian, Dean of Faculty at Colby College, who welcomed those in attendance. Welcoming remarks were also offered by Dr. Miriam Bennett, Professor Emeritus, Department of Biology, Colby College. Following these opening remarks, President Burtt introduced the third annual Margaret Morse Nice Plenary Lecture, "Intraspecific variation in the sizes and shapes of birds," presented by Frances C. James. The Nice Lecture was followed by the first business meeting of the Wilson Ornithological Society.

The scientific program included 45 presentations organized into six paper sessions and one session for the 13 poster presentations. Approximately half of all presentations were by students. In addition, there were two workshops, one on post-baccalaureate careers in wildlife and conservation, presented jointly by the Wilson Ornithological Society and the Ornithological Council, and the other on bird skinning, conducted by WOS Librarian Janet Hinshaw.

On Friday evening the conferees enjoyed a "down East" lobster bake at Johnson Pond on the Colby College campus. At the conclusion of this meal, the satisfied decapodivores reconvened for a social at the Cotter Union. Field trips on Friday and Saturday mornings included excursions to Sidney Bog and Colby Arboretum. Several longer field trips were scheduled for Sunday, including birding along coastal sites in southern Maine, white-water rafting on the Kennebec River, birding in the greater Waterville area, and a pelagic trip to Matinicus rock, where those participating viewed Atlantic Puffins (*Fratercula arctica*), Razorbills (*Alca torda*), Black Guillemots (*Cepphus grylle*), and several species of procellariiformids.

A social hour preceded the annual banquet, which was held in Dana Hall. At the conclusion of a fine dinner President Burtt briefly addressed the conferees, commended Herb Wilson and the Local Committee for a pleasant conference venue and Ted Davis and the Scientific Program Committee for a successful meeting, thanked retiring Members of Council Peter Frederick and Danny Ingold for their service to the Society, and recognized all student presenters for their contributions. The following awards were presented:

MARGARET MORSE NICE MEDAL
(for the WOS plenary lecture)

Frances C. James, "Intraspecific variation in the sizes and shapes of birds."

EDWARDS PRIZE
(for the best major article in volume 110 of *The Wilson Bulletin*)

Sheila Conant, H. Douglas Pratt, and Robert J. Shallenberger, 1998, "Reflections on a 1975 expedition to the lost world of the Alaka'i and other notes on the natural history, semantics, and conservation of Kaua'i birds." Wilson Bull. 110:1–22.

LOUIS AGASSIZ FUERTES AWARD

Kazuya Naoki, "Community evolution in the Andean tanagers of the genus *Tangara*."

PAUL A. STEWART AWARDS

Paul M. Brandy, "Olive-sided Flycatcher habitat use in managed landscapes."

Thomas V. Dietsch, "Ecology and conservation of Neotropical birds in coffee agro-ecosystems of southern Mexico."

Amanda D. Rodewald, "Disturbance in forested landscape: influence of type and magnitude on forest birds."

WILSON ORNITHOLOGICAL SOCIETY TRAVEL AWARDS

Thomas V. Dietsch, "Relating Neotropical birds and vegetative structure to certification criteria for coffee agrosystems in Chiappas, Mexico."

Falk Huettmann, "Wintering Razorbills, *Alca torda*, and auk assemblages in the lower Bay of Fundy, Canada. Results from two winter surveys 1997/98 and 1998/99."

Rachael Z. Jennings, "Spatial and temporal variation in the distributions of *Calypte* hummingbirds along an elevational transect, Riverside County, California."

Karl E. Miller, "Nesting success of the Great Crested Flycatcher in natural nests and in nest boxes: predation rates increase with nest box age."

Kimberly A. Peters, "Swainson's Warbler habitat

selection in a managed bottomland hardwood forest in South Carolina."

ALEXANDER WILSON PRIZE
(for best student paper)

Christopher M. Somers, "Bird depredation of grapes in a Niagara Vineyard: do predictable trends exist?"

Selection committee for the Nice Medal–Edward H. Burtt., Jr. (chair), John Kricher, William E. Davis, Jr., and W. Herbert Wilson; for the Edwards Prize–Robert Beason (chair), Charles Blem, and Doris Watt; for the Fuertes and Stewart Awards–Richard Stiel (chair), James Sedgwick, and Kelli Stone; for the Wilson Ornithological Society Travel Award–William E. Davis, Jr. (chair), and John C. Kricher; and for the Wilson Prize–William E. Davis, Jr. (chair), Jon Barlow, Robert Beason, Richard Conner, and Sara Morris.

FIRST BUSINESS MEETING

The first business meeting was called to order by President Burtt at 10:02 on Friday, 11 June, in Room 105 Keyes Hall. Secretary Smallwood then presented to those who had gathered a synopsis of Thursday's council meeting, commenting on the successful efforts of Herb Wilson and the local committee and of Second Vice-president Ted Davis and the scientific program committee. He reviewed the awards offered by the Society, the winners to be announced at the annual banquet, and reported that Council had enthusiastically increased their monetary values: the prestigious Louis Agassiz Fuertes Award increased to $2500, the Margaret Morse Nice Award increased to $1000, and the annual funding for up to four Paul A. Stewart Awards was increased to $2000. Secretary Smallwood informed the membership that to alleviate any confusion over two separate WOS awards made in honor of Margaret Morse Nice, namely the MMN Award for amateur ornithologists and the MMN Medal for ornithologists presenting plenary lectures on a lifetime of ornithological research, the MMN Award would, in the spirit of the contribution of amateurs to the field of ornithology, henceforth be known as the George A. Hall and Harold F. Mayfield Award. Council had also increased the amount of funding available for student travel awards to $5000 annually. Secretary Smallwood announced that Bob Beason had been elected to a third year as Editor of *The Wilson Bulletin,* noting that the journal was not only published under budget, due mostly to format changes and electronic submissions, but also published slightly ahead of schedule. The secretary then reviewed the Conservation Committee report on reauthorization of the Endangered Species Act. The 2000 meeting will be held 27–30 April at Hotel Galvez in Galveston, at the invitation of the Houston Audubon Society and the Gulf Coast Bird Observatory; Dwight Peake will be the local host. The 2001 meeting will be held jointly with the Arkansas Audubon Society, 3–6 May, at the University of Arkansas Continuing Education Center and Fayetteville Hilton; Doug James will chair the local committee.

Although this information was not available at the time of the first business meeting, here the Wilson Ornithological Society honors the memory of WOS members who passed away since the 1998 meeting: Robert E. Ball (North Canton, OH), Roger M. Evans (Winnipeg, MB), Richard R. Graber (Golconda, IL), Frances Hamerstrom (Plainfield, WI), Robert R. Knickmeyer (Hazelwood, MO), H. Elliot McClure (Camarillo, CA), Henri Ouellet (Hull, QC), Edward F. Rivinus (Upper Marlboro, MD), and Charles G. Sibley (Santa Rosa, CA).

The treasurer's report was then presented by Doris Watt.

Bob Beason offered the editor's report.

President Burtt delivered the report of the Nominating Committee for Peter Stettenheim, Chair, who was not able to attend; other committee members included Kenneth Able, Patricia Gowaty, and Ellen Ketterson. The following slate of candidates was offered: President, John C. Kricher; First Vice-President, William E. Davis, Jr.; Second Vice-President, Charles R. Blem; Secretary, John A. Smallwood; Treasurer, Doris J. Watt, and Members of Council for 1999–2002, Robert A. Askins, Gary Ritchison, Charles F. Thompson, and Jeffrey R. Walters.

The first business meeting was adjourned at approximately 10:20

SECOND BUSINESS MEETING

The second business meeting was called to order by President Burtt at 13:31, Saturday, 12 June, in Room 105 Keys Hall, at which time he recalled the report of the nominating committee to the floor. Calling for additional nominations and hearing none, President Burtt accepted a motion from Dick Banks, seconded by Sara Morris, that the nominations be closed. That motion passed unanimously. Jerry Jackson moved that the slate of officers (but not councilors) be passed unanimously by acclimation. After a second from Sara Morris, it was. Because there were four candidates for three seats on the Council (two Members of Council for 1999–2002, and one to complete Charles Blem's 1997–2000 Council term) election was by paper ballot, with the following result: Members of Council for 1999–2002, Robert A. Askins and Jeffrey R. Walters; Member of Council for 1999–2000, Charles F. Thompson.

Dwight Peake, Local Chair, updated those assembled on the 2000 meeting in Galveston. After a brief discussion about the proposed name change for *The Wilson Bulletin,* and remarks on the electronic publication of the *Bulletin* and the *Ornithological Newsletter,* Sara Morris moved for adjournment. Ted Davis and Peter Frederick seconded the motion, and the membership indicated with the appropriate body language that the motion had indeed passed. This occurred shortly before 14:00.

REPORT OF THE TREASURER

1 JULY 1998 THROUGH 30 JUNE 1999

GENERAL FUNDS

Balance Forward		$ 64,264.33
Receipts		
Regular and Sustaining Memberships	$ 29,688.00	
Student Memberships	$ 4,278.00	
Family Memberships	$ 112.00	
Total Dues		$ 34,078.00
Subscriptions	$ 24,005.00	
Newsletter	$ 181.00	
Back Issues	$ 406.25	
Page Charges	$ 16,911.25	
Total Income from Publications		$ 41,503.50
Contributions: Research Fund	$ 291.00	
Van Tyne Library	$ 560.00	
General Endowment	$ 30.00	
Life, Patrons (Gen Endowment)	$ 1,000.00	
Unrestricted	$ 937.00	
Total Contributions		$ 2,818.00
Royalties	$ 1,127.70	
Interest from Checking Account	$ 490.52	
Interest from Endowments	$ 24,573.16	
Dividends from Dreyfus Acct (reinvested)	$ 999.02	
Subtotal		$ 27,190.40
Miscellaneous		$ 994.35
Net OSNA Adjustment		$ (680.41)
TOTAL RECEIPTS		$ 105,903.84
Disbursements		
Bulletin Publication		
June 1998	$ 17,191.67	
September 1998	$ 16,280.53	
December 1998	$ 18,239.61	
March 1999	$ 16,570.33	
Editor's expenses	$ 4,315.07	
Total Publication Costs		$ 72,597.21
OSNA Expenses	$ 5,921.00	
Officer's expenses	$ 253.95	
CPA (tax filing)	$ 465.00	
Incorporation fee	$ 5.00	
Editor's honorarium	$ 2,000.00	
Editor's travel	$ 500.00	
Library	$ 1,000.00	
Miscellaneous	$ 81.80	
Total Operating Expenses		$ 10,226.75
Organizational Awards	$ 1,700.00	
Ornithological Council Contribution	$ 1,000.00	
ABC Dues	$ 150.00	
Total Philanthropies		$ 2,850.00
TOTAL DISBURSEMENTS		$ 85,673.96
Ending Balance		$ 84,494.21

CASH ACCOUNTS

First Source Bank Checking 1 July 99	$ 61,832.05	
Dreyfus Liquid Assets 1 July 99	$ 22,662.16	
Total Cash on Hand		$ 84,494.21
Van Tyne Library Accounts		
Starting Balance	$ 2,531.63	

Receipts	$ 8,788.79	
Expenses	$ (3,046.13)	
Ending Balance		$ 8,274.29

SUTTON DESIGNATED ACCOUNT

Endowment Principal as of 1 July 98	$ 66,956.97	
Increase in Principal Value 98–99*	$ 68,898.72	
1998 Earnings*	$ 1,998.06	
Funds disbursed for Color Plates (2)	$ 1,935.00	
Balance		$ 63.06

TOTAL ENDOWMENT FUNDS

1996 Market Value	$ 676,029.00
1997 Market Value	$ 814,315.00
1998 Market Value (1 July 98)	$ 968,838.00
1999 Market Value (1 July 99)	$ 1,096,733.81

*Based on 2.9% yield on Mellon account

Doris J. Watt, *Treasurer*

EDITOR'S REPORT—1998

During 1998, the editorial office of *The Wilson Bulletin* received 245 manuscripts including 6 that were provided by Jed Burtt for the Symposium on Neotropical Ornithology. This is a continued increase in the number of manuscripts submitted over the past several years. The acceptance rate was 40% for these manuscripts, similar to that of the past. The review process took an average of 13 weeks and most of manuscripts were returned to the authors with reviewers' comments 2–4 months after receipt. We have been using E-mail for much of the correspondence with authors and reviewers. This has resulted not only in monetary savings from postage, but also has resulted in faster turn around for manuscripts; in some cases the author received a decision within a month of submission.

As a result of the new format and page size of *The Wilson Bulletin,* the journal has gone from approximately 800 pages per volume to 600 pages. The current volume contains the same number of manuscript pages, figures, and tables as previous issues. Most of the difference in length is because many of the figures and tables require less space with the 2-column format than they did with the single column format. The use of electronic manuscript (disk) submission has resulted in fewer corrections in the galley stage. Three issues in 1998 contained color frontispieces and 3 of the 4 issues that are out or in the works for 1999 contain color frontispieces. We have had some problems with the printer to get them to make the frontispieces to bleed to the edge of the paper, but I think those have been resolved.

I greatly appreciate the assistance of the editorial board, Clait Braun, Richard Conner, and Kathy G. Beal for their timely advise on many manuscripts, especially Kathy for her advice on manuscripts with difficult statistical problems and for doing the index. Editorial assistants Tara Baideme, Melanine Daniels, John Lamar, Dante Thomas, and Doris Watt assisted in tracking and checking the many manuscripts. The State University of New York at Geneseo and the Biology Department continue to support the editor and the running of the editorial office in many ways.

Robert C. Beason, *Editor*

The reports of the standing committees are as follows:

REPORT OF THE MEMBERSHIP COMMITTEE

In October 1998, Laurie Goodrich took over as membership chair from John Smallwood, WOS Secretary. Current members of the WOS membership committee are Laurie Goodrich, Chair, Hawk Mountain (PA), Jim Ingold of Louisiana State University (LA), John Smallwood of Montclair State University (NJ), Amanda Rodewald of Pennsylvania State University (PA), Christine Howell of University of Missouri-Columbia (MO), and Daniel Ingold of Muskingum College (OH).

The membership poster was displayed during the last year at the joint OSNA societies meeting in St. Louis (MO), April 1998, the Raptor Research Foundation meeting in Salt Lake City (UT), October 1998, and the Pennsylvania Wildlife Society meeting in Williamsport (PA), March 1999. Brochures were also displayed at a few other meetings, including the Pennsylvania Society of Ornithology in Wellsboro, May 1998.

Since October 1998, the chair has received at least ten inquiries from people who have not received their journal. Most inquiries occurred between March and May. All inquiries have been forwarded to Allen Press and/or the OSNA Director, Anthony Bledsoe. Most people seem to be locating a contact person for membership via the web site. The chair has not received any other inquiries for brochures or information during her tenure.

The membership brochure needs to be reprinted. Before we undertake a large run, the committee would like to have Council review the text and layout, etc., to make any necessary changes. Ideally, we need to

make these changes before the August AOU meeting. Please return all suggestions to Laurie Goodrich or John Smallwood by June 30. If anyone needs a copy of a brochure, please contact Laurie by reply to this e-mail, and she will send one directly. The committee would like to request that any Council Member attending a meeting other than the AOU consider helping out with the display. The chair will ship the poster to the site, and the member would only have to put it up and then repack and ship it back at end of the conference. To volunteer for a meeting, contact Laurie Goodrich, goodrich@hawkmountain.org. If unable to put up a display, please consider taking a stack of brochures for distribution tables.

Lauric J. Goodrich, *Chair*

REPORT OF THE UNDERGRADUATE OUTREACH COMMITTEE

Two people have joined the committee since our last meeting in April, 1998. Thomas Knight of Denver, CO, and Yves de Repentigny, Departement de Sciences Biologiques, Universite de Montreal.

The committee is pleased to announce a *Wilson Bulletin* paper stemming from the workshop on teaching held at the Guelph meeting in 1992. The citation is: Burtt, E. H., Jr., and W. H. Wilson, Jr. 1999. A survey of ornithology courses in North America. Wilson Bull. 111:287–293.

The Guide to Graduate Programs in Ornithology that the Committee has compiled continues to be a valuable resource for undergraduates seeking to pursue graduate research in ornithology. The guide can be found on the Wilson Ornithological Society home page (http://www.ummz.lsa.umich.edu/birds/studies.html). Some users have found that the information provided for some programs is outdated. The committee will be working this year on updating the material in the on-line guide.

Jed Burtt continues to compile laboratory exercises in ornithology. These exercises will be made available at a reasonable cost for any instructor requesting them.

W. Herbert Wilson, Jr., *Chair*

REPORT OF THE JOSSELYN VAN TYNE MEMORIAL LIBRARY COMMITTEE

I am very pleased to be the new Chair of the Josselyn Van Tyne Memorial Library (JVTML) Committee. As such I would like to take this opportunity to thank William A. Lunk for his tireless leadership of the Library Committee. He has been chair of this committee for 40 years. Since 1958 many changes have occurred (e.g., computers have become a standard research tool) and under Dr. Lunk's chairmanship the Library has grown and modernized along with the times. Dr. Lunk deserves our heart-felt thanks for helping to ensure that the Library has been able to provide WOS members and others with ornithological information that they need. During my tenure as chair, I hope to do as good a job, but I do not think I will be able to do it for 40 years!

My philosophy for managing the JVTML has two parts. First, the Library needs to continue acquiring volumes, thereby ensuring that it stays current and thus as useful as possible. Second, it needs to be as accessible as possible to WOS members and others, while maintaining the integrity of the Library.

With respect to acquiring volumes, the following has happened over the past calendar year:

- Loans of library materials to members included 102 transactions to 46 people or institutions. These loans included 417 books, journals and photocopied articles, with many of the articles going to authors of BNA accounts.
- A total of 201 publications were received from 167 organizations or individuals. These included 120 exchanges, 23 subscriptions, and 24 gifts.
- A few journals have been added, primarily from Africa, and others dropped because they have either ceased or merged.
- 758 items were donated by members and friends. These donations included 17 books, 522 journal issues, and 219 reprints, reports and misc. items.
- 17 members and friends donating materials included: C. Braun, D. Klem, Jr., J. Hinshaw, O. Komar, J. Marks, R. Meek, R. Payne, D. Pioli, W. Post, W. J. Richardson, T. Shane, J. Spendelow, R. Tashian, E. Walters, R. Whiting, J. Youngman, and H. Zernickow.
- Five institutions also donated materials: L. Birch for the Edward Grey Institute of Field Ornithology, J. Buki for the Hungarian Institute of Ornithology, L. Kiff for the Peregrine Fund, F. Lohrer for Archbold Biological Station, and G. Penn for Point Reyes Bird Observatory.
- New items purchased for $781.52 from the New Book Fund and for the $742.88 credit with Buteo Books included 19 books, journal issues, CD's and tapes.
- The sale of 209 books, 45 journal issues and 5 color plates, all of which were duplicates, resulted in $5,082.30 plus a credit of $2900 with Buteo Books.
- Gifts to other institutions included 216 journal issues to Hungarian Institute of Ornithology, 38 journal issues to Walter Thiede, and 3 journal issues to The Peregrine Fund.

As to the accessibility of the materials to members and others, the following has been accomplished:

- The web site (http://www.ummz.lsa.umich.edu/birds/wos.html) continues to be enhanced. Journals currently received are listed on the site as well as how to access the University of Michigan's on-line catalogue, which can be used to check holdings.
- The large number of duplicate books for sale from Helen Lapham's bequest will soon be listed on the web. When it is available, a notice will be posted in the OSNA Newsletter.

Due to lack of space, we need to reduce our stock of back issues of *The Wilson Bulletin.* We plan to keep around 50 to 75 copies of each issue where possible. We would like to sell (give away, actually) surplus copies for the cost of postage and handling. Thus far we have "sold" over 1300 issues. Certainly we do not want surplus issues to end up in the recycle bin and ideally we would like these issues to go to institutions in lesser developed countries. I do not know the best way to determine which institutions could use them. Any ideas to help us solve this problem would be most appreciated.

Needs for the 1999/2000 academic year:

- We need help in identifying institutions in lesser developed countries that could use copies of back issues. We currently have surplus copies of most issues, which will allow us to provide nearly complete runs.
- An additional part-time student is needed to help the Library work to reduce significantly its surplus of back issues of the *Bulletin,* to get more information up on the web, and to send out the large numbers of orders we will hopefully generate (via the web) from members and friends wanting to buy duplicate copies from Helen Lapham's bequest. I do not know the particulars of how to obtain funds to hire a student. I assume that funds would need to be run through the University of Michigan, which would mean overhead would be applied. The amount of overhead would depend on what the Society's bylaws say or what is customary for the Society to pay. (The full indirect-cost rate at the University is 52.5%, but can range from that to 0%, depending on what the funder requires.) We would like to have a student who works at $7.00 an hour for an average of 15 hours a week over 11 months, and with 8.55% in benefits (i.e., FICA). Thus a total of $5,000 (direct cost) would be needed. Certainly if we can find a work/study student, then we would need only around 2/3 of that or $3,400. We anticipate that sales from Helen Lapham's bequest will provide that amount of money and more, but it will not be available ahead of time.

My job has been quite easy due to the help of Janet Hinshaw, who manages the day-to-day tasks in the Library. Indeed, she is the one who provided me with the figures I am reporting below.

In closing, I want to offer my thanks to those people who make the JVTML work so efficiently: Joann Constantinides, the secretary for the Bird Division in the Museum of Zoology, who handles many of the library requests; Kari Chciuk, the library work/study student, who for 2 years has handled most of the day-to-day filing and routine jobs, as well as sorting thousands of reprints; and of course to THE most important person connected with the Library, Janet Hinshaw, who provided me with the figures I reported above and who literally "runs the show" by making sure the library is kept up-to-date, and as useful to members and friends as possible. All of these people make my job quite easy.

Terry L. Root, *Chair*

The Committee on the Scientific Program, consisting of William E. Davis, Jr., chair, and John C. Kricher, presented the following program, assisted by session moderators and workshop organizers Edward H. Burtt, Jr., Richard N. Conner, Janet Hinshaw, Jerome A. Jackson, Sara R. Morris, John A. Smallwood, and Susan M. Smith.

PAPER SESSIONS

D. J. Albano, Univ. of Massachusetts, Amherst, MA, "Partial migration in the Belted Kingfisher (*Ceryle alcyon*)."

J. C. Barlow and S. N Leckie, Royal Ontario Museum, Toronto, ON, Canada, "Winter frugivory in Gray Vireos—do eastern populations eat berries too?"

R. E. Brown, USFWS Southern Research Station, Nacogdoches, TX, "Habitat, nest site, and nest box selection by the Prothonotory Warbler in eastern Texas."

R. N. Conner, D. Saenz, and D. C. Rudolph, Southern Research Station, Nacogdoches, TX, "The value of Red-cockaded Woodpecker cavity trees for studying initial attack of pines by southern pine beetles."

R. L. Curry and J. Wotanis, Villanova Univ., Villanova, PA, "Northward movement of the Carolina/Black-capped Chickadee contact zone in southeastern Pennsylvania: inferences from song patterns."

T. V. Dietsch and A. H. Mas, Univ. of Michigan, Ann Arbor, MI, "Relating Neotropical birds and vegetative structure to certification criteria for coffee agroecosystems in Chiapas, Mexico."

P. C. Frederick, Univ. of Florida, Gainesville, FL, "Community structure and population dynamics of breeding wading birds in the Everglades."

M. J. Forman, E. H. Burtt, Jr., and J. M. Ichida, Ohio Wesleyan Univ., Delaware, OH, "Microorganisms in the plumage of Galliformes."

M. J. Hartley, Univ. of Maine, Orono, ME, "Effects of partial cutting on avian community composition."

F. Huettmann, Atlantic Cooperative Wildlife Ecology Research Network, Fredericton, NB, Canada, "Wintering Razorbills, *Alca torda,* and auk assemblages in the lower Bay of Fundy, Canada. Results from two winter surveys 1997/98 and 1998/99."

J. M. Ichida, J. M. Mann, and E. H. Burtt, Jr., Ohio Wesleyan Univ., Delaware, OH, "The nest, the nestling, and the microbe."

J. A. Jackson, Whitaker Center, Florida Gulf Coast Univ., Ft. Myers, FL, and W. E. Davis, Jr., Boston Univ., Boston, MA, "Great Egrets, catfish, and the economics of birds and humans."

R. Z. Jennings, Univ. of Texas., Austin, TX, "Spatial

and temporal variation in the distributions of *Calypte* hummingbirds along an elevational transect, Riverside County, CA."

J. M. Jonas and J. A. Smallwood, Montclair State Univ., Upper Montclair, NJ, "The influences of weather and migration pressure on the growth of nestling American Kestrels in northwestern New Jersey."

E. L. Kershner, J. W. Walk, and R. E. Warner, Univ. of Illinois, Urbana, IL, "The effect of predator removal on grassland bird nest success."

D. L. King, R. M. DeGraaf, USDA Forest Service Northeastern Forest Experiment Station, and C. R. Griffin, Univ. of Massachusetts, Amherst, MA, "Do predation rates on artificial nests accurately reflect predation rates on natural bird nests?"

P. A. McDowell, J. M. Ichida, and E. H. Burtt, Jr., Ohio Wesleyan Univ., Delaware, OH, "*Streptomyces* and the evolution and microecology of avian plumage."

K. E. Miller, Univ. of Florida, Gainesville, FL, "Nesting success of the Great Crested Flycatcher in natural nests and in nest boxes: predation rates increase with nest box age."

J. J. Nocera and P. D. Taylor, Acadia Univ., Wolfville, NS, Canada, "Behavior of failed and non-breeding Common Loons during the summer breeding season."

K. A. Peters, North Carolina State Univ., Raleigh, NC "Swainson's Warbler habitat selection in a managed botttomland hardwood forest in South Carolina."

Z. Richards and D. Capen, Univ. of Vermont, Burlington, VT, "Landscape effects on the Black-throated Blue Warbler (*Dendroica caerulescens*): a comparison of demographics in large forest isolates and contiguous forest."

D. C. Rudolph, R. N. Conner, R. H. Johnson, W. G. Ross, S. J. Burgdorf, R. R. Schaefer, and D. Saenz, Southern Research Station, Nacogdoches, TX, "Red-cockaded Woodpecker cavity trees, southern pine beetle mortality, and pine resin characteristics."

D. Saenz, R. N. Conner, C. S. Collins, and D. C. Rudolph, Southern Research Station, Nacogdoches, TX, "Long-term use of artificial cavities by Red-cockaded Woodpeckers in eastern Texas."

J. A. Sedgwick, Biological Resources Div., Fort Collins, CO, "Geographic variation in the song of the Willow Flycatcher."

C. M. Somers and R. D. Morris, Brock Univ., St. Catharines, ON, Canada, "Bird depredation of grapes in a Niagara vineyard: do predictable trends exist?"

R. Stiehl and A. Farmer, Midcontinent Ecological Science Center, Fort Collins, CO, "Richness of Piping Plover foraging habitat on Fire Island, NY."

J. W. Walk, E. L. Kershner, and R. E. Warner, Univ. of Illinois, Urbana, IL, "Area and age of habitat patches and nesting success in grassland birds."

J. R. Walters, Virginia Polytechnic Institute and State Univ., Blacksburg, VA, "Experimental studies of effects of cavities on territory quality in Red-cockaded Woodpeckers."

W. H. Wilson, Jr., Colby College, Waterville, ME, "Arrival dates of Maine migratory breeding birds: a trans-century comparison."

POSTERS

R. C. Banks, National Museum of Natural History, Washington, DC, "Variation in Greater White-fronted Geese in the Central Flyway."

M. T. Bradley and S. R. Morris, Canisius College, Buffalo, NY, "Is tail feather shape a reliable indicator of age in warblers and thrushes?"

E. H. Burtt, Jr., and P. Y. Burtt, Ohio Wesleyan Univ., Delaware, OH, "Ice damage to feathers."

M. Carey and J. Mills, Univ. of Scranton, Scranton, PA, "Nest-site selection and breeding biology of Field Sparrows in a rapidly changing old field habitat."

M. C. Herceg, J. A. Weiner, and S. R. Morris, Canisius College, Buffalo, NY, "A seasonal comparison of the stopover patterns and behavior of migratory passerines on Appledore Island, Maine."

J. H. Hull and A. R. Buckelew, Jr., Bethany College, Bethany, WV, "Group anting in the Common Grackle."

J. L. Ingold, Louisiana State Univ., Shreveport, LA, "Winter birds of small remnant prairies in the Piney Woods of northern Louisiana."

E. D. Kennedy and A. McCauley, Albion College, Albion, MI, "Acquisition by Albion College of prints from 10 original copper plate engravings used in Alexander Wilson's "American Ornithology"."

G. J. Robertson, G. Chapdelaine, and R. D. Elliot, Canadian Wildlife Service, A. W. Diamond and F. Huettmann, Univ. of New Brunswick, Fredericton, NB, Canada, "Population status and trends of Razorbills in Canada."

C. R. Smith, J. T. Weber, and M. E. Richmond, Cornell Univ., Ithaca, NY, "Using gap analysis information to guide planning for conservation of birds in New York state: a comparison of science-based and expert-opinion approaches."

D. Westmoreland and M. Moseley, US Air Force Academy, Colorado Springs, CO, "The cost of bright egg coloration in American Robin nests."

D. W. White and E. D. Kennedy, Albion College, Albion, MI, "Do House Wrens identify target eggs by sight or by feel?"

J. B. Whittier and D. M. Leslie, Jr., US Geological Survey, Biological Resources Division, Oklahoma Cooperative Fish and Wildlife Research Unit, Oklahoma State Univ., Stillwater, OK, "The effect of drought on nest success in Least Terns."

ATTENDANCE

COLORADO: *Fort Collins,* Jim Sedgwick, Dick Stiehl; *Colorado Springs,* David Westmoreland.

CONNECTICUT: *New Britain,* Sylvia Halkin; *Sharon,* Elyse Glover.
DISTRICT OF COLUMBIA: *Washington,* Dick Banks.
FLORIDA: *Fort Myers,* Jerry Jaekson; *Gainesville,* Mary Clench, Peter Frederiek, Karl Miller; *Tallahassee,* Fran James.
ILLINOIS: *Bushell,* Larry Hood; *Centralia,* Prieilla McDowell; *Collinsville,* Kimberly Peters; *Grayslake,* Scott Hiekman; *Urbana,* Eric Kershner, Jeffrey Walk.
INDIANA: *Notre Dame,* Doris Watt.
KANSAS: *Manhattan,* Dave Rintoul.
LOUISIANA: *Shreveport,* James Ingold.
MAINE: *Bar Harbor,* Goodale Wing; *Belgrade,* Don Mairs; *Fairfield,* Miriam Bennett; *Farmington,* Sarah Sloane; *Orono,* Mitsehka Hartley; *Richmond,* Peter Vickery; *Unity,* Ed Beals; *Waterville,* Larkspur Morton, Neal Taylor, Herb Wilson; *Wilton,* Wendy Howes.
MARYLAND: *Chevy Chase,* Ellen Paul; *St. Mary's City,* Ernie Willoughby.
MASSACHUSETTS: *Boston,* Ted Davis; *South Hadley,* Susan Smith.
MICHIGAN: *Albion,* Dale Kennedy, Doug White; *Ann Arbor,* Tom Dietsch; *Chelsea,* Janet Hinshaw; *Kalamazoo,* Riehard Brewer.
NEW HAMPSHIRE: *Keene,* Jon Atwood; *West Swazey,* Lewis Kibler.
NEW JERSEY: *Belleville,* Jeffrey Jonas; *Cape May,* Tom Parsons; *Edison,* Robert Colburn; *Upper Montclair,* John Smallwood.
NEW YORK: *Buffalo,* Sara Morris; *Cheetkowaga,* Jeanette Weiner; *Geneseo,* Bob Beason; *Grand Island,* Maria Bradley; *Ithaca,* Charles Smith; *Johnson City,* Michael Herceg; *Utica,* Judy Melntyre.
NORTH CAROLINA: *Asheville,* Lou Weber; *Chapel Hill,* Helmut Mueller, Naney Mueller.
OHIO: *Columbus,* Sandy Gaunt, Toby Gaunt; *Delaware,* Jed Burtt, Martin Forman, Jann Ichida; *Sunbury,* Kathy Wildman.
OKLAHOMA: *Stillwater,* Joanna Whittier.
PENNSYLVANIA: *Berwyn,* Phil Street; *Doylestown,* Jennifer Niese; *Kempton,* Laurie Goodrich; *Scranton,* Miehael Carey; *Villanova,* Bob Curry; *Swarthmore,* Janet Williams.
RHODE ISLAND: *Wakefield,* Ceeil Kersting.
TEXAS: *Austin,* Raehel Jennings; *Belton,* John Cornelius; *Galveston,* Dwight Peake; *Nacogdoches,* Raymond Brown, Diek Conner, Craig Rudolph, Dan Saenz.
VERMONT: *Northfield,* Bill Barnard.
VIRGINIA: *Arlington,* Marcus Koenen; *Blacksburg,* Jeff Walters.
WEST VIRGINIA: *Bethany,* Jay Buekelew; *Morgantown,* George Hall.
CANADA: *Fredericton New Brunswick,* Falk Huettman; *St. Catherine's Ontario,* Christopher Somer; *Toronto Ontario,* Jon Barlow, Sheridan Leckie; *Wolfville Nova Scotia,* Joseph Noeera.

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Acknowledgments

The following individuals graciously served as referees for the volume of *The Wilson Bulletin*. I am deeply grateful for their assitance and advice—Robert C. Beason, Editor.

C. S. Adkisson, D. G. Ainley, J. L. B. Albuquerque, T. Alworth, E. Ammon, D. Anderson, J. G. T. Anderson, T. R. Anderson, B. A. Andres, C. D. Ankney, R. D. Applegate, D. Arcese, W. J. Arendt, F. Arengo, K. A. Arnold, R. A. Askins, J. E. Austin, M. L. Avery, M. C. Baker, N. E. Baldaccini, R. C. Banks, D. R. Barber, F. K. Barker, J. R. Bart, J. M. Bates, E. Bayne, K. G. Beal, D. L. Beaver, J. C. Bednarz, B. M. Beehler, S. R. Beissinger, L. D. Beletsky, J. R. Belthoff, W. Belton, T. M. Bergin, P. W. Bergstrom, S. L. Berman, L. B. Best, J. Bielefeldt, K. L. Bildstein, M. A. Bishop, J. G. Blake, C. R. Blem, W. M. Block, J. Blondel, C. W. Boal, C. E. Bock, E. K. Bollinger, E. S Botelho, R. Bowman, G. T. Braden, C. E. Braun, J. D. Brawn, R. M. Brigham, D. J. Bright-Smith, M. C. Brittingham, E. W. Brooks, B. T. Brown, C. R. Brown, K. M. Brown, A. H. Brush, T. Brush, A. Burger, D. E. Burhans, B. E. Byers, V. J. Byre, D.F. Caccamise, L. D. Caldwell, S. B. Canale, R. A. Canterbury, T. Caraco, M. D. Carey, T. W. Carpenter, N. R. Carrie, E. L. Caton, E. Chamberlain, B. R. Chapman, M. K. Chase, A. R. Clark, R. G. Clark, L. M. Coburn, J. A. Collazo, D. M. Collister, R. N. Conner, P. G. Connors, C. J. Conway, F. Cooke, C. J. Counard, R. J. Craig, D. A. Cristol, J. F. Cully, R. L. Curry, D. R. Curson, T. W. Custer, F. J. Cuthbert, T. V. Dailey, G. C. Daily, S. J. Daniels, M. P. Darveau, W. B. Davison, D. K. Dawson, R. D. Dawson, B. Day, S. Debus, R. M. Degraaf, J. R. Des Lauriers, T. DeSanto, T. L. Devault, A. W. Diamond, V. M. Dickison, D. R. Diefenbach, R. H. Diehl, T. V. Dietsch, J. J. Dinsmore, R. C. Dobbs, S. L. Dodd, T. Donovan, A. W. Doolittle, S. Dove, R. D. Drobney, D. C. Duffy, J. R. Duncan, J. B. Dunning, C. R. Dykstra, S. W. Eaton, J. R. Eberhard, L. S. Eberhardt, M. E. Eddins, W. R. Eddleman, R. T. Engstrom, A. J. Erskine, R. M. Erwin, C. Estades, M. R. Evans, T. J. Evans, J. R. Faaborg, S. Faccio, G. H. Farley, G. Farnsworth, M. B. Fenton, E. J. Finck, L. D. Flake, D. J. Flaspohler, P. L. Flint, T. B. Ford, M. S. Foster, A. D. Fox, A. B. Franklin, J. D. Fraser, H. Freifeld, L. E. Friesen, R. W. Furness, S. W. Gabrey, J. L Ganey, K. L. Garrett, R. J. Gates, A. S. Gaunt, D. G. Gawlik, F. R. Gehlbach, R. P. Gerhardt, J. C. Gering, J. A. Gessaman, H. G. Gilchrist, C. E. Gill, S. Gill, J. Glahn, R. S. Gnam, N. M. Gobris, M. Gochfeld, C. B. Goguen, T. Goldsmith, G. Gooding, L. J. Goodrich, C. E. Gordon, B. M. Gottfried, C. Graham, W. Gram, J. G. Granlund, C. L. Gratto-Trevor, G. A. Green, C. H. Greenberg, J. S. Greenlaw, J. W. Grier, C. R. Griffin, C.S. Griffiths, K. Groschupf, T. C. Grubb, R. Grundel, J. A. Grzybowski, K. J. Gutzwiller, S. J. Hackett, J. H. Haffer, T. M. Haggerty, S. M. Haig, J. P. Hailman, F. R. Hainsworth, D. A. Hall, M. J. Hamas, P. B. Hamel, I. K. Hanski, R. G. Harper, M. J. Hartley, D. Haskell, E. W. Hein, H. T. Hendrickson, C. J. Henny, G. R. Hepp, J. R. Herkert, F. Hertel, S. K. Herzog, D. O. Hill, S. L. Hilty, A. Holmes, D. W. Holt, P. D. Hooper, J. P. Hoover, S. L. Hopp, D. J. Horn, C. S. Houston, J. D. Hubbard, J. Hughes, W. G. Hunt, D. J. T. Hussell, R. L. Hutto, L. D. Igl, D. J. Ingold, M. L. Isler, F. M. Jaksic, D. A. James, F. C. James, R. A. James, A. P. Jaramillo, R. L. Jarvis, D. A. Jenni, W. E. Jensen, D. H. Johnson, L. S. Johnson, M. D. Johnson, J. Jolivette, I. L. Jones, J. Jones, K. L. Jones, S. Jones, D. G. Jorde, S. M. Joy, R. Kane, T. L. Kast, W. Kendall, R. A. Kennamer, E. D. Kennedy, P. L. Kennedy, D. M. Keppie, L. H. Kermott, H. Khanna, A. A. Kinsey, M. Klaassen, P. K. Kleintjes, J. T. Klicka, D. S. Klute, R. W. Knapton, M. T. Koenen, W. D. Koenig, R. R. Koford, O. Komar, N. Krabbe, A. W. Kratter, D. G. Krementz, J. C. Kricher, K. S. Kritz, D. E. Krodsma, J. D. Lambert, R. B. Lanctot, R. S. Lange, D. V. Lanning, W. E. Lanyon, S. Lariviere, B. Lauro, J. J. Lawler, P. E. Lederle, M. R. Lein, R. E. Lemon, R. A. Lent, M. L. Leonard, D. J. Levey, E. T. Linder, B. D. Linkhart, C. D. Littlefield, J. P. Loegering, B. A. Loiselle, E. R. Loos, P. E. Lowther, R. C. Lundquist, J. E. Lyons, T. R. Mace, R. H. F.

Macedo, R. E. Maier, T. J. Maier, B. P Maransky., M. A. Marin, M. A. Marini, J. S. Marks, C. D. Marti, P. M. Mayer, H. L. Mays, J. C. Mazourek, K. M. Mazur, T. McCoy, K. P. McFarland, W. B. McGillivray, J. W. McIntyre, K. McKay, M. R. McLandress, D. B. McNair, R. McNeil, S. M. Melvin, B. D. Meyburg, J. M. Meyers, E. H. Miller, K. E. Miller, B. A. Millsap, M. Milonoff, D. Mock, A. P. Møller, R. Montgomery, D. Moore, F. R. Moore, D. C. Morimoto, S. R. Morris, M. L. Morrison, S. G. Mosa, R. S. Mulivihill, M. T. Murphy, J. J. Negro, D. A. Nelson, S. A. Nesbitt, G. J. Niemi, M. Nogales, E. Nol, C. J. Norment, R. L. Norton, J. P. O'Neill, P. Olsen, L. W. Oring, C. P. Ortega, H. Ouellet, R. B. Owen, K. C. Parsons, D. N. Pashley, C. A. Paszkowski, P. W. Paton, R. B. Payne, G. Pendelton, C. M. Perrins, B. G. Peterjohn, T. A. Peterson, J. Picman, P. J. Pietz, W. H. Piper, B. J. Ploger, D. W. Pogue, W. Post, B. Poulin, A. N. Powell, H. W. Power, S. Pribil, R. O. Prum, K. L. Purcell, W. H. Pyle, P. Radewald, S. A. Raouf, J. H. Rappole, S. E. Reinert, D. L. Reinking, L. Reitsma, J. V. Remsen, M. K. Reynolds, R. E. Ricklefs, R. S. Ridgely, C. M. Riley, J. D. Rising, G. Ritchison, J. H. Rivera, C. S. Robbins, M. B. Robbins, G. J. Robertson, W. D. Robinson, N. L. Rodenhouse, H. M. Rogers, R. N. Rosenfield, R. R. Roth, S. I. Rothstein, S. M. Russell, M. R. Ryan, D. Saenz, L. Santisteban, R. A. Sargent, G. Sattler, J. A. Savidge, T. L. Scarlett, P. F. Schempf, A. Scheuerlein, S. R. Schmidt, J. K. Schmutz, G. D. Schnell, E. A. Schreiber, T. Schulenberg, D. Schulter, J. A. Sedgwick, G. Seutin, C. E. Shackelford, D. H. Shedd, M. A. Shields, W. G. Shriver, M. Siders, T. R. Simons, C. G. Sims, J. A. Smallwood, C. R. Smith, D. G. Smith, J. N. M. Smith, M. K. Sogge, S. S. Soukup, D. A. Spector, J. A. Spendelow, S. F. H. Spofford, D. W. Steadman, K. Steenhof, M. A. Stern, R. B. Stiehl, C. M. Stinson, S. H. Stoleson, D. F. Stotz, P. C. Stouffer, W. D. Svedarsky, D. L. Swanson, P. W. Sykes, D. A. Tallman, W. K. Taylor, D. L. M. Teixeira, R. C. Telfair, E. J. Temeles, G. D. Therres, G. R. Thomas, C. F. Thompson, C. W. Thompson, J. E. Thompson, S. C. Thompson, T. L. Tibbits, M. E. Tobin, T. Tracy, C. L. Trine, J. D. Tyler, T. J. Underwood, C. Van Riper, W. M. Vander Hagen, D. W. Verser, P. D. Vickery, M. A. Villard, G. H. Visser, C. M. Vleck, K. H. Voous, F. Vuilleumier, S. J. Wagner, J. W. Walk, G. E. Walsburg, C. Ward, D. Ward, I. G. Warkentin, K. S. Warner, B. D. Watts, L. M. Weber, L. C. Wemmer, C. G. West, G. B. West, D. Westmoreland, C. J. Whelan, D. Whitacre, C. M. White, M. J. Whitfield, R. C. Whitmore, D. A. Wiedenfeld, F. A. Wilkinson, D. E. Willard, J Williams, L. E. Williams, C. N. Willis, W. Wiltschko, J. C. Wingfield, D. W. Winkler, M. Winter, L. L. Wolf, D. H. Wolfe, P. B. Wood, P. W. Woodward, B. L. Woodworth, A. L. Wright, R. H. Yahner, P. H. Yaukey, Y. Yom-Tov, R. Yosef, S. Zack, G. D. Zenitsky, M. C. Zicus

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By Kathleen G. Beal

This index includes references to genera, species, authors, and key words or terms. In addition to avian species, references are made to the scientific names of all vertebrates mentioned within the volume and other taxa mentioned prominently in the text. Nomenclature follows the AOU Check-list of North American Birds (1998). Reference is made to books reviewed, and announcements as they appear in the volume.

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  effect of wind turbines on upland nesting birds, 100–104
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